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A REVISION OF *TRISETUM*, *PEYRITSCHIA*, AND *SPHENOPHOLIS* (POACEAE: POOIDEAE: AVENINAE) IN MEXICO AND CENTRAL AMERICA[1]

Victor L. Finot,[2] Paul M. Peterson,[3] Robert J. Soreng,[3] and Fernando O. Zuloaga[4]

Abstract

A taxonomic treatment of *Trisetum*, *Peyritschia*, and *Sphenopholis* for Mexico and Central America is given. In Mexico and Central America four species of *Peyritschia*, two species of *Sphenopholis*, and 17 species of *Trisetum* s. str. are recognized. *Peyritschia deyeuxioides* and *P. pringlei* range from Mexico to Ecuador, *P. koelerioides* is found in southern Mexico to Guatemala, and *P. humilis* is endemic to Mexico. *Sphenopholis obtusata* ranges from Canada to the U.S.A. and Mexico, whereas *S. interrupta* is found in the southwestern U.S.A. and Baja California, Mexico. Mexico has the largest number of *Trisetum* species at 15, and nine of these are endemic. Five species of *Trisetum* are found in Guatemala, three in Costa Rica and Panama, and a single species is found in Honduras and the Dominican Republic. A new subgenus *Deschampsioidea* (Louis-Marie) Finot in *Trisetum* is proposed. Four new species of *Trisetum* from Mexico are described and illustrated: *T. durangense* Finot & P. M. Peterson, *T. martha-gonzaleziae* P. M. Peterson & Finot, and *T. spellenbergii* Soreng, Finot & P. M. Peterson (all in subg. *Deschampsioidea*); and *T. ligulatum* Finot & Zuloaga (in subg. *Trisetum*, sect. *Trisetaera*). Keys for the genera, subgenera, sections, and species of *Trisetum*, *Peyritschia*, and *Sphenopholis* that occur in Mexico and Central America are given. The names *Trisetum gracile* E. Fourn. and *Trisetum* subsect. *Deschampsioidea* Louis-Marie are lectotypified.

Key words: Aveninae, Gramineae, *Peyritschia*, Poaceae, Pooideae, *Sphenopholis*, *Trisetum*.

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Resumen

Se presenta un tratamiento taxonómico de los géneros *Trisetum*, *Peyritschia* y *Sphenopholis* para México y América Central. Cuatro especies de *Peyritschia*, dos especies de *Sphenopholis* y 17 especies de *Trisetum* s. str. fueron reconocidas en México y Centroamérica. *Peyritschia deyeuxioides* y *P. pringlei* habitan desde México a Ecuador, *P. koelerioides* se encuentra desde el sur de México hasta Guatemala y *P. humilis* es endémica de México. *Sphenopholis obtusata* se encuentra en Canadá, EE. UU. y México, mientras *S. interrupta* habita el sudoeste de EE. UU. y Baja California, México. México posee el mayor número de especies de *Trisetum*, 15 especies, nueve de ellas endémicas. Cinco especies de *Trisetum* se encuentran en Guatemala, tres en Costa Rica y Panamá y sólo una en Honduras y República Dominicana. Se propone un nuevo subgénero *Deschampsioidea* (Louis-Marie) Finot en *Trisetum*. Cuatro nuevas especies de *Trisetum* de México son descritas e ilustradas: *T. durangense* Finot & P. M. Peterson, *T. martha-gonzaleziae* P. M. Peterson & Finot y *T. spellenbergii* Soreng, Finot & P. M. Peterson (todas en subg. *Deschampsioidea*); y *T. ligulatum* Finot & Zuloaga (en subg. *Trisetum*, sect. *Trisetaera*). Se presentan claves para los géneros, subgéneros, secciones y especies de *Trisetum*, *Peyritschia* y *Sphenopholis* presentes en México y América Central. Los nombres *Trisetum gracile* E. Fourn. y *Trisetum* subsect. *Deschampsioidea* Louis-Marie fueron lectotipificados.

Trisetum Pers. comprises about 70 species in temperate regions of Europe, Asia, America, Australia, and New Zealand (Louis-Marie, 1928–1929; Hitchcock, 1939; Swallen, 1948; Tsvelev, 1970, 1983; Jonsell, 1980; Veldkamp & Van der Have, 1983; Clayton & Renvoize, 1986; Pohl & Davidse, 1994, 2002; Edgar, 1998; Soreng et al., 2003). A general account of the American taxa of *Trisetum* was published by Louis-Marie (1928–1929), in which he recognized a total of 60 species. Hitchcock (1939) recognized 19 species of *Trisetum* in North America, including Mexico. There are 38 species of *Trisetum* in North, Central, and South America (Finot, 2003b). With the noteworthy exception of the cosmopolitan *T. spicatum* (L.) K. Richt., most species of *Trisetum* have a rather restricted geographical distribution. The majority of the species are from Mexico, where 9 are endemic, and only *T. irazuense* (Kuntze) Hitchc. extends from Mexico and Central America to Ecuador in South America.

The systematic relationships of the Mexican and Central American species of *Trisetum* are not well known, in part due to the close affinity with *Peyritschia* E. Fourn. and *Sphenopholis* Scribn. Fournier (1886) described the genus *Peyritschia* with one species from Mexico and Guatemala, *P. koelerioides* (Peyr.) E. Fourn. Hitchcock (1939) also recognized *Peyritschia* in his treatment of the North American flora. Koch (1979) transferred to *Peyritschia* a second species from Mexico, Costa Rica, and Guatemala, *Deschampsia pringlei* Scribn. [= *P. pringlei* (Scribn.) S. D. Koch]. Hernández-Torres and Koch (1987) did not recognize *Peyritschia* and placed both of these species in *Trisetum*. The systematic position of these two species in *Trisetum* has not gained universal acceptance, although some recent treatments recognize *Peyritschia* (Clayton & Renvoize, 1986; Watson & Dallwitz, 1992; Finot, 2003a). One further species, *Peyritschia conferta* (Pilg.) Finot, occurs in Venezuela, Ecuador, and Bolivia. *Peyritschia* differs from *Trisetum* in having 1-nerved glumes, lemmas with bilobed apices that are awnless, mucronate, or with a well-developed awn borne near the base, paleas that are tightly enclosed by the margins of the lemma, and florets with only two stamens. *Trisetum* has a first glume 1- to 3-nerved, a second glume 3- to 5-nerved, lemma apices with 2 to 4 short awns with the central awn inserted above the middle of the lemma, paleas that are not tightly enclosed by the lemma (i.e., gaping), and florets with 3 stamens.

Sphenopholis was described by Scribner (1906) to include seven species and seven subspecies. He characterized the genus as having spikelets that disarticulate below the glumes and between the florets, second glumes that are usually broadly obovate, and lemmas with an entire or 2-toothed apex that is awnless or awned just below the apex. In contrast, *Trisetum* has spikelets that disarticulate above the glumes and between the florets, second glumes that are lanceolate to ovate, and lemmas with a biaristulate to bidentate apex that is awned on the upper third. On the basis of these characters, Scribner (1906) transferred three species of *Trisetum* to the new genus *Sphenopholis*: *S. interrupta* (Buckley) Scribn., *S. hallii* (Scribn.) Scribn., and *S. palustris* (Michx.) Scribn. Hitchcock (1939) and Hitchcock and Chase (1951) retained these three species in *Trisetum*, although Hitchcock (1915) earlier placed *S. palustris* as a synonym of a fourth species, *S. pensylvanica* (L.) Hitchc. Erdman (1965) also recognized *S. pensylvanica* but did not include *S. interrupta*, although he recognized that this species resembles *Sphenopholis* in spikelet disarticulation.

Steudel (1854), who recognized four species, made one of the earliest enumerations of *Trisetum* in Mexico: *T. deyeuxioides* (Kunth) Kunth, *T. elongatum* (Kunth) Kunth, *T. tolucense* (Kunth) Kunth, and *T. viride* (Kunth) Kunth. An important contribution to the knowledge of Mexican species was made by Fournier (1886), who described six new species: *T. gracile* E. Fourn., *T. nivosum* E. Fourn., *T. interruptum* E. Fourn., *T. paniculatum* E. Fourn., *T. bambusiforme* E. Fourn., and *T. virletii* E. Fourn. On the basis of Pringle's collections from Mexico, Scribner in Beal's (1896) *Grasses of North America* described three new taxa: *T. deyeuxioides* var. *pubescens* Scribn. ex Beal, *T. filifolium* Scribn. ex Beal var. *filifolium*, and *T. filifolium* var. *aristatum* Scribn. ex Beal. In a general synopsis of Mexican grasses, Hitchcock (1913) described *T. palmeri* Hitchc. and mentioned nine other species. By the middle of the 20th century, most Mexican species of *Trisetum* had been described. More recently, Morden and Valdés-Reyna (1983) described a new species, *T. curvisetum* Morden & Valdés-Reyna, endemic to Nuevo León, Mexico.

Hernández-Torres and Koch (1988) have published the most recent revisionary study for all Mexican species of *Trisetum*, and they recognized 11 species: *T. altijugum* (E. Fourn.) Scribn., *T. curvisetum*, *T. deyeuxioides*, *T. filifolium*, *T. interruptum*, *T. irazuense*, *T. kochianum* Hern. Torres, *T. pringlei*, *T. spicatum*, *T. viride*, and *T. virletii*. Espejo-Serna et al. (2000), as a part of the floristic list of Mexican monocotyledons, mentioned for southern Mexico the presence of *T. angustum* Swallen and *T. pinetorum* Swallen, both originally described from Guatemala. Other recent treatments of the genus are those of McVaugh (1983) for Nueva Galicia, Herrera-Arrieta (2001) for Durango, and Herrera and Rzedowski (2001) for Valle de Mexico.

In Central America, Pohl (1980) in *Flora Costaricensis* mentioned four species: *Trisetum deyeuxioides*, found also from Mexico to Central and South America, *T. irazuense*, *T. pringlei* from Mexico to Central America, and *T. tonduzii* Hitchc. known only from Costa Rica and Panama. McVaugh (1983) and Hernández-Torres and Koch (1988) cited *T. viride* from Guatemala, and Hernández-Torres and Koch (1988) cited *T. kochianum* from Guatemala and Costa Rica.

The only subgeneric treatment of *Trisetum* in the Americas was done by Louis-Marie (1928–1929), who prepared a key to the subgenera, sections, and subsections. His *Trisetum* subg. *Heterolytrum* Louis-Marie sect. *Anaulacoa* Louis-Marie included: *T. filifolium*, *T. interruptum* (as *T. disjunctum* Louis-Marie), *T. irazuense*, *T. rosei* Scribn. & Merr., *T. spicatum*, *T. viride* (as *T. paniculatum* E. Fourn.), and *T. virletii*. In subsection *Sphenophoidea* Louis-Marie he placed *Sphenopholis interrupta* (as *T. interruptum*); in subsection *Deschampsioidea* Louis-Marie he placed *T. palmeri*; in subsection *Graphephorum* (Desv.) Louis-Marie he placed *Peyritschia koelerioides* [as *T. altijugum* (E. Fourn.) Scribn.], and *T. pringlei*; in subgenus *Isolytrum* Louis-Marie he placed *Peyritschia deyeuxioides* (Kunth) Finot (as *T. deyeuxioides*) and *T. viride*.

Here, we describe and illustrate four new Mexican species of *Trisetum* (*T. durangense* Finot & P. M. Peterson, *T. martha-gonzaleziae* P. M. Peterson & Finot, *T. spellenbergii* Soreng, Finot & P. M. Peterson, and *T. ligulatum* Finot & Zuloaga), and we discuss the systematics for *Trisetum*, *Peyritschia*, and *Sphenopholis* in Mexico and Central America. We also include a subgeneric classification of the species in *Trisetum* for Mexico and Central America.

Material and Methods

This study is based on the examination of herbarium specimens from BAA, BAF, C, CIIDIR, CONC, CR, P, QCA, US, S, SI, including the type specimens of most of the species studied. For anatomical observations, hand cross sections were made from the central portion of the blade below the flag leaf, and surface features were observed on the adaxial portion of the ligule. Abaxial epidermis preparations were made according to the method in Metcalfe (1960). Slides were observed on a Zeiss microscope at SI.

Key for Distinguishing *Trisetum*, *Sphenopholis*, and *Peyritschia*

1a. Stamens 2; glumes linear, isomorphic, 1-nerved; lemmas awnless or awned with a 2-lobate apex; palea tightly enclosed by the margins of the lemma (not gaping) ..... *Peyritschia*

1b. Stamens 3; glumes lanceolate, ovate-lanceolate, or oblanceolate, heteromorphic, first glume 1- to 3-nerved, second glume 3- to 5-nerved; lemmas with 2 to 4 short awns at the apex or entire or 2-toothed; palea not tightly enclosed by the margins of the lemma (gaping).

2a. Perennials; disarticulation between the florets and above the glumes; upper glumes lanceolate to ovate-lanceolate ..... *Trisetum*

3a. Lemma apex opaque, the intermediate nerves extended beyond the apex as two short awns; awn inserted on the upper third of the lemma ..... *Trisetum* subg. *Trisetum*

4a. Panicle lax, ± open, ovate to pyramidal ..... *Trisetum* sect. *Trisetum*

4b. Panicle narrow, spiciform ..... *Trisetum* sect. *Trisetaera*

3b. Lemma apex hyaline, without nerves or with both intermediate and marginal nerves extended beyond the apex as four short awns; awn inserted on the middle of the lemma ..... *Trisetum* subg. *Deschampsioidea*

2b. Annuals or perennials; disarticulation of florets below the glumes; upper glumes oblanceolate to obovate ..... *Sphenopholis*

Taxonomic Treatments

Sphenopholis Scribn., Rhodora 8: 142. 1906. TYPE: *Sphenopholis obtusata* (Michx.) Scribn.

Annuals or perennials, without rhizomes; culms 20–120 cm tall, glabrous. Leaf sheaths glabrous or sparsely pubescent; ligule membranous; blades 1–12 mm wide, glabrous or sparsely pubescent, flat, soft. Inflorescence in panicles 5–25 cm long, lax and narrow. Spikelets 2- or 3-flowered; pedicels short and glabrous; disarticulation below the glumes; glumes heteromorphic, usually shorter than the spikelet; first glume narrow, shorter than or as long as the second glume, linear-lanceolate, 1-nerved; second glume obovate to oblanceolate, 3- to 5-nerved; lemmas smooth or scabrous, muticous or awned, 3- to 5-nerved, blunt to biaristate at the apex; awn, when present, borne on the upper third of the lemma; callus glabrous to subglabrous; palea 2-keeled, shorter than its lemma; lodicules 2, membranous, minutely dentate at the apex, 0.5 mm long; stamens 3, anthers 0.5–1 mm long; ovary glabrous. Caryopsis with liquid endosperm.

Sphenopholis is a small genus with five species from Canada to Mexico (Clayton & Renvoize, 1986). Erdman (1965) revised *Sphenopholis* and recognized four species in addition to the hybrid *Sphenopholis* ×*pallens* (Biehler) Scribn. [*S. obtusata* (Michx.) Scribn. × *S. pensylvanica* (L.) Hitchc.]. Two species are represented in Mexico and Central America.

Key to the Species of *Sphenopholis* in Mexico and Central America

1a. Lemmas awned, the awns 4–8 mm long; spikelets 4–6 mm long ..... 1. *S. interrupta*

1b. Lemmas unawned; spikelets 1.5–3.6 mm long ..... 2. *S. obtusata*

1a. Sphenopholis interrupta (Buckley) Scribn. subsp. **interrupta,** Rhodora 8: 145. 1906. Basionym: *Trisetum interruptum* Buckley, Proc. Acad. Nat. Sci. Philadelphia 14: 100. 1862. TYPE: U.S.A. Middle Texas, *Buckley s.n.* (lectotype, designated by Hitchcock (1935: 973), PH not seen.; isotype, US-fragment & photo ex PH!).

Avena elongata Kunth, Nov. Gen. Sp. 1: 148. 1816. *Trisetarium elongatum* (Kunth) Poir., Encycl. 5: 366. 1817. *Trisetum elongatum* (Kunth) Kunth, Rev. Gram. 1: 101. 1829. TYPE: Mexico. In scopulosis prope urbem Mexico, 1833, *Bonpland s.n.* (holotype, P!; isotype, US-3102206 ex B!).

Calamagrostis longirostris Buckley, Prelim. Rep. Surv. Texas 2. 1866. TYPE: U.S.A. Texas. [No type material has been located. Although the type locality is presumed to be Texas, Buckley did not cite a locality nor did he mention a collector in his original protologue.]

Trisetum hallii Scribn., Bull. Torrey Bot. Club 11: 6. 1884. *Sphenopholis hallii* (Scribn.) Scribn., Rhodora 8(92): 146. 1906. *Trisetum interruptum* UNRANKED *hallii* (Scribn.) Hitchc. TYPE: U.S.A. Texas: prairies Houston, 1872, *Hall 799* (holotype, US-72664!).

Annual; culms 10–40 cm tall, glabrous, mostly 3 nodes, the nodes glabrous. Leaf sheaths glabrous or sparsely pubescent, with one side extended upward, shorter than internodes; ligules 1 mm long, truncate, ciliate, pilose on the dorsal surface; blades 3–10 cm × 1–4 mm, flat. Panicles 5–12 cm × 4–15 mm, narrow. Spikelets 4–6 mm long, 2- or 3-flowered; rachilla sparsely pubescent; glumes 3.5–5 mm long, about equal in length and equaling or shorter than the spikelet, glabrous, scaberulous along the keel; first glume linear-lanceolate, 3-nerved; second glume obovate to oblanceolate, 5-nerved; lemmas 3.5–5 mm long, lanceolate, glabrous, 3- to 5-nerved, 2-aristulate at the apex, awned on the upper third of the lemma; awn 4–8 mm long, slightly twisted and twice geniculate; palea 2–2.5 mm long, about half the length of the lemma, 2-nerved, the nerves scabrous, 2-dentate at the apex; callus glabrous to subglabrous; lodicules 0.5 mm long, slightly bilobate at the apex, the lobes rounded, obtuse to acute. Anthers about 0.5 mm long.

Distribution. U.S.A. and Mexico. According to Gould and Moran (1981), *Sphenopholis interrupta* is widely distributed in the southwestern United States.

Specimens studied. MEXICO. **Baja California:** near U.S. Boundary, "Northern Lower California," 1 Apr. 1886, *C. R. Orcutt 1431* (US).

Key to the Subspecies of *Sphenopholis interrupta*

1a. Glumes glabrous ..... *S. interrupta* subsp. *interrupta*

1b. Glumes pubescent ... *S. interrupta* subsp. *californica*

1b. Sphenopholis interrupta subsp. **californica** (Vasey) Scribn., Rhodora 8: 146. 1906. Basionym: *Trisetum californicum* Vasey, U.S.D.A. Div. Bot. Bull. 13(1): t. 46. 1892. *Trisetum interruptum* Buckley var. *californicum* (Vasey) Louis-Marie, Rhodora 30: 240. 1929. TYPE:

Mexico. Northern Lower California, *C. R. Orcutt 1437* (lectotype, designated by Hitchcock (1939: 552) and Hernández-Torres & Koch (1988: 80), US-868402!; isotype, MO-2526390 not seen).

Glumes pubescent, the trichomes 0.1–0.4 mm long.

Distribution. *Sphenopholis interrupta* subsp. *californica* was described for Northern Lower California, and its distribution seems to be restricted to the type locality.

Notes. Hitchcock (1939) designated the lectotype for *Trisetum californicum* without explicitly citing the herbarium. Hernández-Torres and Koch (1988) then specifically designated the US sheet as the lectotype.

Comments. Though the systematic position of this taxon in *Sphenopholis* was proposed by Scribner (1906), subsequent treatments by Louis-Marie (1928–1929), Hitchcock and Chase (1951), and Erdman (1965) excluded this species from *Sphenopholis.* According to Erdman (1965) further study is needed to clarify the generic placement of this species. On the basis of micromorphological characters of lemma epidermes of several genera in Aveninae, including *Trisetum* and typical species of *Sphenopholis,* Finot and Matthei (unpublished results) support the generic position of this species in *Sphenopholis.* Louis-Marie (1928–1929) created *Trisetum* subsect. *Sphenophoidea* for species that disarticulate below the glumes and included in this *T. interruptum, T. interruptum* var. *californicum, T. hallii, T. pensylvanicum* (L.) P. Beauv., *T. palustre* (Michx.) Torr., and *T. ludovicianum* Vasey. We believe that all of these species belong in *Sphenopholis.*

2. Sphenopholis obtusata (Michx.) Scribn., Rhodora 8(92): 144. 1906. Basionym: *Aira obtusata* Michx., Fl. Bor. Amer. 1: 62. 1803. *Airopsis obtusata* (Michx.) Desv., J. Bot. appl. 1: 200. 1808. *Poa obtusata* (Michx.) Link, Hort. Berol. 1: 76. 1827. *Agrostis obtusata* (Michx.) Steud., Nomencl. Bot. ed. 2, 1: 41. 1840. *Koeleria obtusata* (Michx.) Trin. ex Steud., Nomencl. Bot. ed. 2, 1: 41. 1840. *Reboulea obtusata* (Michx.) A. Gray, Manual 591. 1848. *Eatonia obtusata* (Michx.) A. Gray, Manual ed. 2, 558. 1856. TYPE: U.S.A. Florida: *Michaux s.n.* (lectotype, designated by Hitchcock (1908: 152), P!, photo NY not seen & US!; isotype, US-72667-fragment!).

Aira truncata Muhl., Descr. Gram. 83. 1817. *Koeleria truncata* (Muhl.) Torr., Fl. N. Middle United States 1: 116. 1823. TYPE: U.S.A. Pennsylvania: *H. C. Muhlenberg 127* (holotype, PH not seen; isotype, US-1535792-fragment!).

Koeleria paniculata Nutt., Gen. N. Amer. Pl. 2: (Add. 2). 1818. TYPE: U.S.A. East Florida, *T. Say s.n.* (holotype, PH not seen, photo US!; isotype, US-fragment!).

Reboulea gracilis Kunth, Revis. Gram. 2: 341, t. 84. 1830, nom. illeg. TYPE: *Michaux s.n.* (holotype, B not seen; isotypes, P!, US-76319-fragment ex B!).

Trisetum lobatum Trin., Mem. Acad. Imp. Sci. St.-Petersbourg, Ser. 6, Sci. Math. 1: 66. 1830. *Sphenopholis obtusata* subsp. *lobata* (Trin.) Scribn., Rhodora 8: 144. 1906. *Sphenopholis obtusata* var. *lobata* (Trin.) Scribn. ex B. L. Rob., Rhodora 10: 65. 1908. TYPE: Ad flumen rubrum (Red River), America borealis (holotype, LE-TRIN-2437.01!).

Eatonia densiflora E. Fourn., Mexic. Pl. 2: 111. 1886. *Aira mexicana* Trin. ex E. Fourn., Mexic. Pl. 2: 111. 1886, nom. inval. TYPE: U.S.A. Texas: Bejar, Feb. 1839, *J. L. Berlandier 1617* (holotype, W not seen; isotypes, B not seen, LE-TRIN-1951.02!, US-72668-fragment!).

Eatonia obtusata var. *robusta* Vasey ex L. H. Dewey, Contr. U.S. Natl. Herb. 2: 544. 1894. *Eatonia robusta* (Vasey ex L. H. Dewey) Rydb., Bull. Torrey Bot. Club 32: 602. 1905. *Sphenopholis robusta* (Vasey ex L. H. Dewey) A. Heller, Muhlenbergia 6: 12. 1910. TYPE: U.S.A. Texas: Wallisville, 1881, *Wallis s.n.* (holotype, US!; isotype, NY not seen).

Eatonia obtusata var. *robusta* Vasey ex Rydb., Contr. U.S. Natl. Herb. 3(3): 190. 1895, nom. illeg. hom. TYPE: U.S.A. Nebraska: Mullen, *P. A. Rydberg 1807* (holotype, not located; isotypes, NY, US!).

Eatonia obtusata var. *purpurascens* Vasey ex Rydb. & Shear, Bull. Div. Agrostol. U.S.D.A. 5: 30. 1897. *Sphenopholis obtusata* var. *lobata* fo. *purpurascens* (Vasey ex Rydb. & Shear) Waterf., Rhodora 50: 93. 1948. TYPE: U.S.A. Oklahoma: False Washita, 1868, *E. Palmer 404* (lectotype, designated by Hitchcock (1935: 956), US-868756!).

Eatonia pubescens Scribn. & Merr., Bull. Div. Agrostol. U.S.D.A. 26: 6. 1900. *Sphenopholis obtusata* subsp. *pubescens* (Scribn. & Merr.) Scribn., Rhodora 8: 144. 1906. *Sphenopholis obtusata* var. *pubescens* (Scribn. & Merr.) Scribn. ex B. L. Rob., Rhodora 10: 65. 1908. *Sphenopholis pubescens* (Scribn. & Merr.) A. Heller, Muhlenbergia 6: 12. 1910. *Reboulea obtusata* var. *pubescens* (Scribn. & Merr.) Farw., Rep. Michigan Acad. Sci. 17: 181. 1916. TYPE: U.S.A. Mississippi: Starkeville, 30 Apr. 1891, *S. M. Tracy s.n.* (holotype, US-72670!).

Eatonia annua Suksd., W. Amer. Sci. 15: 50. 1906. *Sphenopholis annua* (Suksd.) A. Heller, Muhlenbergia 6: 12. 1910. TYPE: U.S.A. Oregon: Wasco Co., Dalles on Columbia River, 8 June 1897, *W. N. Suksdorf 1553* (isotypes, F not seen, GH not seen, ISC not seen, NY not seen, UC not seen, US-72671!).

Annual; culms 20–120 cm tall. Leaf sheaths glabrous, scabrous, or finely pubescent; blades 8–15 cm × 3–12 mm, flat. Panicles 5–25 cm × 5–20 mm, narrow. Spikelets 1.5–3.6 mm long, 2- or 3-flowered; rachilla mostly glabrous; glumes 1–3(–3.6) mm long, about equal in length, dimorphic,

shorter than the spikelet, scaberulous especially along the keel; first glume linear-lanceolate, 1-nerved; second glume conspicuously obovate, 3-nerved; lemmas 1.8–2.8 mm long, lanceolate, glabrous to scaberulous, entire at the apex, unawned; callus glabrous; anthers 0.5–0.7 mm long.

Anatomy and micromorphology. Ligule apices with papillose cells and short, stiff trichomes; ligule epidermis composed of long cells with straight walls; stomata absent; macrohairs absent; prickles present. Foliar epidermis with long cells rectangular to fusiform, with sinuate lateral walls; short cells present in costal zones only, rectangular, with sinuous walls; trichomes absent; stomata present.

Specimens studied. MEXICO. **Coahuila:** Diaz, Rio Grande Valley, 17 Apr. 1900, *C. G. Pringle 8285* (US); Villa Union, 20 Apr. 1965, *F. W. Gould 11136* (US); Muzquiz, Santa Elana City Park, 24 Apr. 1965, *F. W. Gould 11227* (US). **Distrito Federal:** vicinity of Mexico, 27–30 July 1910, *A. S. Hitchcock 5893*. **Durango:** city of Durango & vicinity, June 1896, *E. Palmer 255* (US). **Guanajuato:** 2 km NE of San Miguel, 31 Oct. 1952, *E. R. Sohns* 500 (US). **Nuevo León:** Monterrey, 6–8 June 1910, *A. S. Hitchcock 5571* (US). **Oaxaca:** Oaxaca, 12, 13 Aug. 1910, *A. S. Hitchcock 6166* (US). **Puebla:** Rancho Posada, 20 May 1910, *Nicolas s.n.* (US); *G. Arsene s.n.* (US). **Sonora:** Alamos, 1890, *E. Palmer 577* (US).

Peyritschia E. Fourn., Mexic. Pl. 2: 109. 1886. TYPE: *Peyritschia koelerioides* (Peyr.) E. Fourn.

Perennials, with or without rhizomes; culms 20–200 cm tall, mostly glabrous. Leaf sheaths glabrous or pubescent; blades flat; ligule membranous. Inflorescence in panicles narrow, contracted, spiciform or lax and somewhat open. Spikelets 2-flowered; rachilla glabrous to copiously pubescent; disarticulation above the glumes and between the florets; glumes isomorphic, 1-nerved, equal or subequal, as long as the spikelet or longer; lemmas bilobed at the apex, awned near the base or the middle of the lemma, rarely muticous or shortly mucronate near the tip (*P. koelerioides* mucronate or muticous); palea tightly enclosed by the margins of the lemma (not gaping), 2-keeled; stamens 2; lodicules 2, membranous; ovary glabrous. Caryopses with liquid endosperm.

Key to the Species of *Peyritschia* in Mexico and Central America

1a. Lemma without a dorsal awn, apex muticous or with a subapical mucro ..... 2. *P. koelerioides*
1b. Lemma with a dorsal awn, borne near the middle or upper third of the lemma, the awn geniculate and extended beyond the glumes.
2a. Rachilla copiously pubescent, the trichomes 2–3 mm long ..... 1. *P. deyeuxioides*
2a. Rachilla pubescent, the trichomes only 0.2–0.8 mm long.
3a. Culms 5–12 cm tall; leaf blades 2.5–3.5 cm long; panicles about 2.5 cm long, 0.5 cm wide, contracted, narrow ..... 3. *P. humilis*
3b. Culms 20–200 cm tall; leaf blades 5–15 cm long; panicles 5–20 cm long, 1–3(–4) cm wide, narrow but relatively open ..... 4. *P. pringlei*

1. **Peyritschia deyeuxioides** (Kunth) Finot, Contr. U.S. Natl. Herb. 48: 478. 2003. Basionym: *Avena deyeuxioides* Kunth, Nov. Gen. Sp. 1: 147. 1816. *Trisetaria deyeuxioides* (Kunth) Poir., Encycl. Suppl. 5: 366. 1817. *Trisetum deyeuxioides* (Kunth) Kunth, Rev. Gram. 1: 102. 1829. *Deyeuxia triflora* Nees, Linnaea 19: 691. 1847. TYPE: Mexico. "Ad ripam Lacus Tezcucensis," *Humboldt & Bonpland s.n.* (holotype, P!; isotypes, BM not seen, LE-TRIN-1913.05!, US-865589 fragment ex P!).

Avena trichopodia J. Presl, Reliq. Haenk. 1: 254. 1830. TYPE: Mexico. *Haenke s.n.* (holotype, PR not seen; isotypes, LE-TRIN-1945.01a!, US-0865583 fragment ex PR!).

Deyeuxia evoluta E. Fourn., Bull. Soc. Bot. France 24: 181. 1877. *Trisetum evolutum* (E. Fourn.) Hitchc., Contr. U.S. Natl. Herb. 17: 325. 1913. TYPE: Mexico. Veracruz: Mirador, 1841, *F. M. Liebmann 730* (lectotype, designated by Hitchcock (1939: 557) and Hernández-Torres & Koch (1988: 78), US-207459!; isotypes, C not seen, LE!, MO-3056872!, P not seen).

Trisetum deyeuxioides var. *pubescens* Scribn. ex Beal, Grasses N. Amer. 2: 374. 1896. TYPE: Mexico. Michoacán: dry hills near Patzcuaro, 19 Nov. 1891, *C. G. Pringle 3950* (holotype, MSC not seen; isotypes, BM not seen, ENCB not seen, MEXU not seen, MO-3056871 not seen, P!, US-868407!).

Perennial, without rhizomes; culms 50–180 cm tall, glabrous. Leaf sheaths glabrous or pubescent; ligule 1–3(–5) mm long, truncate, erose, glabrous; blades 0.5–4 mm wide, flat, narrow toward apex, glabrous or sparsely pubescent, sometimes densely pubescent. Panicles 10–35 × 1–5 cm, lax, somewhat open and nodding. Spikelets 4.5–8 mm long, 2- or 3-flowered; rachilla copiously pubescent, the trichomes 2–3 mm long; glumes (3.5–)4–5.5(–8) mm long, equal, shorter or longer than the florets, linear; first glume with a green midnerve, purplish otherwise, the margins usually hyaline, the keel scabrous; lemmas 4–6 mm long, glabrous, terete, rounded in cross section, 5-nerved, nerves inconspicuous, dorsally awned near the middle or upper third of the lemma; apex entire, bilobed or bidentate; awn 4.5–8(–12) mm long, geniculate and twisted, purple, scabrous; callus short pubescent,

the trichomes 0.3–1 mm long; paleas 2.5–3.5 mm long; lodicules 0.5 mm long, linear, narrow, irregularly lobed at the apex; anthers 1.3–1.7 mm long. Caryopses 1.8–2.5 mm long.

Chromosome number. $2n = 14, 28$ (Tateoka, 1962; Hernández-Torres & Koch, 1988).

Anatomy. Leaf blades are slightly keeled in transverse section, abaxial ribs not well developed, furrows less than one half of the leaf thickness; vascular bundles of first and second order with adaxial and abaxial girders, bundles of third order with adaxial and abaxial strands; marginal sclerenchyma present; bulliform cells large, conspicuous, in fan-shaped groups at the base of adaxial furrows; abaxial epidermis with long rectangular to fusiform intercostal cells; costal zone with cork cells and silica bodies in short rows or more rarely in cork cell-silica body pairs; prickles present.

Distribution. Mexico to Ecuador [Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico (Aguascalientes, Chiapas, Chihuahua, Distrito Federal, Durango, Guerrero, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Queretaro, San Luis Potosí, Veracruz, Zacatecas), Nicaragua, Panama, Venezuela] (Pohl & Davidse, 1994; Finot, 2003a) in humid prairies and open woods, 1000–2600 m.

Notes. Hitchcock (1939) designated the lectotype for *Deyeuxia evoluta* without explicitly citing the herbarium. Hernández-Torres and Koch (1988) then specifically designated the US sheet as the lectotype.

Comments. Based on 25 morphological characters, Koch (1979) pointed out that *P. deyeuxioides* shows an intermediate position between *Peyritschia* and *Trisetum*. However, the androecium is composed of only two stamens, the glumes are 1-nerved, the lemma is terete and dorsally awned near the middle, the apex of the lemma is bilobed, and the palea is tightly enclosed by the margins of the lemma. These characters indicate that this species should be placed in *Peyritschia*.

Specimens studied. COSTA RICA. **Cartago:** Cordillera Central, Volcán Irazú, 2 km NW Sanitorio Durán, 19 Nov. 1968, *Pohl & Davidse 11449* (CR). MEXICO. **Chihuahua:** 19.6 km W of Balleza & 74.2 km E of Guachochi, 18 Sep. 1991, *Peterson et al. 10752* (US); 24.2 km S of San Juanito & 4.8 km N of Creel on MEX 127, 10 Sep. 1989, *Peterson et al. 8007* (US); 122.5 km W of La Junta & 56.7 km W of Tomochic in Parque Nacional Cascada de Basaseachic, 1 Oct. 1989, *Peterson & King 8231* (US); canyons of Sierra Madre, 13 Oct. 1887, *Pringle 1432* (US); Sierra Madre Occidental, Parque Natural Barranca del Cobre, 13.6 mi. NE of La Bufa on road toward Samachique, 31 Oct. 1995, *Peterson et al. 13575* (US). **Coahuila:** Sierra Madre Oriental, 5 mi. W of Chapultepec on cutoff road between Hwy. 54 & 57, 23 mi. S of Saltillo, 16 Oct. 1995, *Peterson & Knowles 13276* (US); ca. 5 km E of Salltillo (Las Palapas) up camino de Quatro, 20 Sep. 2003, *Peterson et al. 17868* (CIIDIR, US). **Distrito Federal:** Desierto de Los Leones, 19 Oct. 1960, *Tateoka 1152* (US). **Durango:** 4.2 km of San Miguel de La Michilia, 24 Sep. 1991, *Peterson et al. 10913* (US); 16.1 km NW of MEX 40 on logging road to Santo Domingo, 5 Oct. 1989, *Peterson & King 8288* (US); 20 mi. SE of Mesquital on road to Charcos, 7 Nov. 1995, *Peterson et al. 13632* (US). **Hidalgo:** boggy margins of Lago Atexca below Molango, 24 July 1947, *H. E. Moore Jr. 3466* (US). **México:** Valle de Mexico, 10 June 1901, *Pringle 8512* (P), *Shaffner 15* (P); prope Tacubaya, *Shaffner 319* (P). **Michoacán:** 13.5 km SE of Zacapu on MEX 15 km toward Quiroga, 1 Oct. 1991, *Peterson et al. 10994* (US). **Morelia:** San Miguel, 8 Aug. 1912, *Arsènes 8645* (P). **Oaxaca:** on Huantla Road 19 km from Teotitlan, 6 Nov. 1963, *McKee 10869* (P). **Querétaro:** 16 mi. E of Landa, 12 Dec. 1960, *Smitchfield & Johnston s.n.* (US). **San Luis Potosí:** between Puerta Huerta and Rioverde in the Sierra de Alvarez, 11 Sep. 1954, *Sohns 1177* (US); near Puerta Huerta in the Sierra de Alvarez, 4 Sep. 1954, *Sohns 1034* (US).

2. Peyritschia koelerioides (Peyr.) E. Fourn., Mexic. Pl. 2: 110. 1886. *Aira koelerioides* Peyr., Linnaea 30: 5. 1859. *Deschampsia koelerioides* (Peyr.) Benth., J. Linn. Soc., Bot. 19: 96. 1881. TYPE: Mexico. México: Volcan de Toluca, 8800 ft., 1846, *C. Heller 311* (holotype, P not seen; isotype, US-1647945-fragment ex P-DRAKE!).

Graphephorum altijugum E. Fourn., Mexic. Pl. 2: 111. 1886. *Trisetum altijugum* (E. Fourn.) Scribn., Rhodora 8(89): 89. 1906. TYPE: Mexico. Veracruz: in monte Orizabensi, 12,000–14,000 ft., *F. M. Liebmann 603* (holotype, P not seen; isotype, US-734835!).

Perennial, rhizomes absent; culms 25–85 cm tall, glabrous; nodes 2 or 3, glabrous. Leaf sheaths glabrous, rarely pubescent, shorter than the internodes; ligule 1–3 mm long, truncate, erose; blades 1.5–4 mm wide, usually glabrous, flat. Panicles 7–20 cm × 4–8(–10) mm, spiciform; rachis and pedicels scabrous. Spikelets 3–5 mm long, 2-flowered; rachilla glabrous to sparsely pubescent, the trichomes less than 0.5 mm long; glumes 3–5 mm long, lanceolate to ovate-lanceolate, equal, longer than the florets, 1-nerved; lemmas 2.5–4 mm long, glabrous, terete, dorsally rounded, 5-nerved; apex bilobed, the lobes short, obtuse, muticous or with a mucro about 1 mm long or less borne near the apex; callus glabrous or short pubescent, trichomes less than 0.5 mm long; paleas 2.4–3.8 mm long; anthers 0.5–1.3 mm long. Caryopses 1.5–3.5 mm long.

Chromosome number. $2n = 28$ (Tateoka, 1962; Hernández-Torres & Koch, 1988).

Micromorphology. Ligule apices have papillate cells and short trichomes, the epidermis with more or less rectangular long cells, hooks, and trichomes; no stomata were seen.

Distribution. Southern Mexico (México, Michoacán, Oaxaca, Veracruz) and Guatemala (Pohl & Davidse, 1994; Finot, 2003a), 2400–4300 m.

Specimens studied. MEXICO. **México:** 20 km al NE de Texcoco, sobre la carretera a Calpulalpán, 10 Oct. 1965, *Rzedowski 21417* (US); Sierra Las Cruces, 1 Oct. 1892, *Pringle 4306* (US); Amecameca, carretera al Paso de Cortés, 20 km al E de la desviación a la carretera a Cuautla, 14 km al ESE de Amecameca, 18 Oct. 1976, *Koch 76206* (US 2989662); 18 mi. S of Patzcuaro, 20–25 Nov. 1961, *King & Soderstrom 5159* (US); 20 km NE de Texcoco, sobre la carretera a Calpulalpán, no date, *Rzedowski s.n.* (US). **Oaxaca:** Sierra de San Felipe, Aug. 1894, *Pringle 4775* (P). **Puebla:** San Nicolás de los Ranchos, declive E del Paso de Cortes, 3.5 km NE entronque de carretera a Amecameca y camino entre Popocatepetl e Ixtaccihuatl, 15 km ESE de Amecameca, 3 Dec. 1976, *Koch 73309* (US).

3. Peyritschia humilis (Louis-Marie) Finot, Contr. U.S. Natl. Herb. 48: 478. 2003. Basionym: *Trisetum humile* Louis-Marie, Rhodora 30: 244. 1929. *Deyeuxia gracilis* E. Fourn., Mexic. Pl. 2: 106. 1886, nom. illeg., non *Deyeuxia gracilis* Wedd. 1875. TYPE: Mexico. Mirador, *F. M. Liebmann 602* (holotype, C!; isotypes, US-3048345 fragment ex hb. Haun.!).

Perennial; culms 5–12 cm tall. Leaf sheaths flattened; ligule membranous, short, laciniate; blades 2.5–3.5 cm long. Panicles 2.5 × 0.5 cm, contracted, narrow, exserted. Spikelets 4 mm long, 2-flowered; pedicels glabrous; rachilla 0.5 mm long, pilose, the trichomes less than 0.8 mm long; glumes 4 mm long, equal, lanceolate, longer than the spikelet, slightly scabrous on the keel, acute at the apex; lemmas 3–3.5 mm long, terete, awned, the margins involute toward the base, bilobed at the apex, the lobes obtuse; awn 4–5 mm long, inserted from the middle to the lower third on the dorsal surface, twisted and geniculate; callus obtuse, sparsely pilose, trichomes ca. 0.2 mm long; paleas shorter than the lemma and enclosed by the margins of the lemma. Caryopses ca. 2 mm long.

Comments. The type of *Deyeuxia gracilis* E. Fourn. conserved in Copenhagen (C) includes a complete plant, 12 cm tall, and a fragment of the panicle, identified by Hitchcock and Chase as *Trisetum spicatum* (L.) K. Richt. The isotype in US bears the same identification. Hernández-Torres and Koch (1988), who synonymized the species within *T. spicatum*, followed this criterion. The morphology of the spikelets confirms its placement within *Peyritschia*: spikelets 4 mm long, 2-flowered; glumes equal, 1-nerved, longer than the spikelet; lemma with a bilobed apex, the awn geniculate and twisted, inserted near the middle of the lemma; callus with short trichomes; rachilla sparsely pilose; stamens 2; ovary glabrous.

Trisetum humile Louis-Marie was a new name for the illegitimate *Deyeuxia gracilis* E. Fourn. 1886, non Weddel 1875, and therefore we use it as the basionym for the new combination in *Peyritschia*.

4. Peyritschia pringlei (Scribn.) S. D. Koch, Taxon 28: 233. 1979. Basionym: *Deschampsia pringlei* Scribn., Proc. Acad. Nat. Sci. Philadelphia 43: 300. 1891. *Trisetum kochianum* Hern. Torres, Phytologia 61: 454. 1987. TYPE: Mexico. Chihuahua: wet places, pine plains, base of Sierra Madre, 7 Oct. 1987, *C. G. Pringle 1429* (holotype, US-747292!; isotypes, LL not seen, MEXU not seen, MICH not seen, US-867629!, US-821538!, VT not seen).

Perennial, without rhizomes; culms 20–200 cm tall. Leaf sheaths glabrous, rarely pubescent; ligule 0.5–4 mm long, truncate or rounded at the apex; blades 5–15 cm × 1.5–4 mm, flat. Panicles 5–20 × 1–3(–4) cm, narrow but relatively open. Spikelets 4–5.5 mm long, 2- or 3-flowered; rachilla pubescent, the trichomes 0.2–0.8 mm long; glumes 4–5.3 mm long, lanceolate, as long as the florets or longer, apex acute; lemmas 3–4.3 mm long, glabrous, terete, bilobed at the apex, rounded in cross section, awned near the base; awn 4.5–7 mm long, geniculate and twisted, exserted; palea 2.3–3 mm long, shorter than its lemma; anthers 0.8–1 mm long. Caryopses 1.5–1.7 mm long, fusiform-cylindric.

Anatomy and micromorphology. Ligule apices composed only of papillate cells, epidermal long cells rectangular to fusiform, with few hooks and no trichomes; no stomata were seen. Leaf blades in transverse section without a keel, without well-developed ribs, furrows less than one half of the leaf thickness; all vascular bundles, except the marginal ones, with both adaxial and abaxial girders; marginal sclerenchyma absent; abaxial epidermis with rectangular long cells with straight side walls, costal cork cells and silica bodies present, prickle hairs present.

Distribution. Mexico (Aguascalientes, Chihuahua, Chiapas, Durango, Guanajuato, Hidalgo, Jalisco, México, Puebla, Querétaro, San Luis Potosí, Sonora, Tlaxacala), Guatemala, Costa Rica, Venezuela, Ecuador (Espejo-Serna et al., 2000; Fi-

not, 2003a). The documentation of the presence of this species in Venezuela and Ecuador provides new records for the distribution of *Peyritschia pringlei*. It was collected by *Peterson & Judziewicz 9302*, in the Provincia de Bolívar, ca. 3000 m, in the Andes of Ecuador, and by *Peterson & Judziewicz 9477* in Provincia de Loja, Ecuador. Lasser found the species in Mérida, Venezuela, in 1942 (*Lasser 431*). According to Hernández-Torres and Koch (1988) this species also occurs in Guatemala. Elevations range from 1600 to 3270 m.

Specimens studied. COSTA RICA. **Cartago:** Cordillera Central, lower slopes of Volcán Irazú, 1 km below San Juan de Chicoa, 8 Nov. 1968, *Pohl & Davidse 11416* (US). ECUADOR. **Bolívar:** 14.5 km E of Guaranda on road to Río Bamba, 24 May 1990, *Peterson & Judziewicz 9302* (US). **Loja:** 6 km W of Colaisaca on road to Sozoranga, 2 June 1990, *Peterson & Judziewicz 9477* (US). GUATEMALA. **Quezaltenango:** 19 June 1954, *Koninck 137* (US). MEXICO. **Chihuahua:** 85.4 km W of Balleza and 8.8 km E of Guachochi, 19 Sep. 1991, *Peterson et al. 10786* (US); 38.6 km SW of La Junta & ca. 70.8 km N of Creel at Paso Arroyo Ancho crossing, 24 Sep. 1988, *Peterson & Annable 5848* (US); Miñaca, 13 Oct. 1910, *Hitchcock 7762* (US). **Durango:** 45 km W of Durango on Hwy. 40 toward El Salto, 27 Oct. 1995, *Peterson et al. 13489* (US); 2 mi. NW of Charcos on road toward Milpas, 9 Nov. 1995, *Peterson et al. 13679* (US); 24 mi. NE of El Salto on Hwy. 40 toward Durango, 26 Oct. 1995, *Peterson et al. 13471* (US); W of Ciudad Durango, 4 mi. W of El Salto, 27 Aug. 1958, *Reeder & Reeder 3124* (US); 4 mi. E of El Salto, 1 Oct. 1953, *Reeder & Reeder 2561* (US); 20 mi. S of Mezquital, 11 Sep. 2003, *Peterson & F. Sánchez-Alvarado 17729* (CIIDIR, US). **Guanajuato:** 8 km W de San Felipe, 27 Oct. 1952, *Sohns 460* (US). **Hidalgo:** Pachuca, 6–7 Sep. 1910, *Hitchcock 6730* (US); *Hitchcock 6737* (US). **Jalisco:** Sierra Cacoma, 7 mi. NW of Los Volcanes on road toward Mascota, 15 Nov. 1995, *Peterson 13724* (US); Tepatitlán-Guadalajara, 26 Sep. 1946, *Hernández X., Ruppert & Guevara 2694* (US); Zempoala, 15 km N of Ciudad Sahagún & 1 km NE of Zempoala, sobre la carretera a Sta. Maria Tecajete, 26 Aug. 1977, *Koch 77179* (US); Mineral del Chico, Parque Natural El Chico, 17 km al N de la carretera Pachuca–Zacualtipán, 4 Dec. 1977, *Koch 77532* (US). **México:** Toluca, 13 Sep. 1910, *Hitchcock 6889* (US). **Puebla:** San Marcos, railway embankment, 29 Aug. 1910, *Hitchcock 6522* (US); Acajete, El Pinal, a 10 km al E de Acajete, 19°09′N, 97°55′W, 16 Sep. 1988, *Tenorio 15165* (US). **Querétaro:** parte mas alta del cerro Zamorano, Mun. Colon, 13 Nov. 1971, *Rzedowski & McVaugh 173* (US). **San Luis Potosí:** 15–18 July 1910, *Hitchcock 5685* (US); Cañón del Lobo, Sierra de San Miguelito, *Sohns 1162* (US); Puerta Huerta in the Sierra de Alvarez, 4 Sep. 1954, *Sohns 1019* (US). **Tlaxcala:** ca. 3 mi. NE of Tlaxco, 23 Sep. 1953, *Sohns 597* (US). VENEZUELA. **Mérida:** Otra Banda, near Mérida, 22 Sep. 1942, *Lasser 431* (US).

Trisetum Pers., Syn. Pl. 1: 97. 1805. *Trisetarium* Poir., Encycl. Suppl. 5: 365. 1817, nom. superfl. *Acrospelion* Besser ex Schult. & Schult. f., Syst. Veg. Mant. 3: 526, 1827, nom. illeg. superfl. *Rebentischia* Opiz, Lotos 4: 104. 1854, nom. superfl., non P. A. Karsten 1869. TYPE: *Trisetum flavescens* (L.) P. Beauv., Ess. Agrostogr. 88, 153, t. 18, f. 1. 1812.

Rupestrina Prov., Fl. Canad.: 689. 1862. TYPE: *Rupestrina pubescens* Prov. [= *Trisetum spicatum* (L.) Richt.]

Perennials, caespitose, sometimes shortly rhizomatous; culms 5–300 cm tall, erect to geniculate at base, glabrous or pubescent. Leaf sheaths glabrous or pubescent, longer or shorter than the internodes; blades flat, conduplicate, convolute or involute, soft, rarely rigid; ligule membranous. Inflorescence in panicles contracted or open, spiciform, ovate, or pyramidal; the rachis glabrous, scabrous, or pubescent. Spikelets (1)2- to 6-flowered, short pedicellate; rachilla pubescent or glabrous, usually prolonged beyond the upper floret; disarticulation above the glumes and between the florets; glumes heteromorphic, lanceolate to ovate-lanceolate, equal or unequal, first glume 1- to 3-nerved, usually shorter and narrower than the second, second glume 3- to 5-nerved; lemmas lanceolate, (3)5(7)-nerved, usually awned or muticous, with apex and margins hyaline, glabrous or pubescent, slightly keeled and compressed, rarely terete; apex with 2 to 4 short awns, entire, or 2-toothed; central awn from the upper third, rarely the middle, of the subapical portion of the lemma; awn exserted, geniculate or merely divaricate; callus short pilose; palea not tightly enclosed by the margins of the lemma (gaping), 2-keeled, hyaline, usually shorter than the lemma; stamens 3, anthers 0.3–4.5 mm long; lodicules 2, membranous; ovary glabrous or with short and shining trichomes near the apex; endosperm solid or liquid, soft or hard. Caryopses compressed, soft; hylum short, punctiform. Basic chromosome number $x = 7$.

Comments. Our subgeneric treatment of the species that occur in Mexico and Central America includes two subgenera: *Trisetum* subg. *Trisetum* and *T.* subg. *Deschampsioidea*, and two sections in subgenus *Trisetum:* section *Trisetum* and section *Trisetaera* (Appendix 1). In the following key we have indicated what subgenus and/or section most species occur in (see leads 5a, 5b, 6a, and 8a).

Key to Species of *Trisetum* in Mexico and Central America

1a. Lemmas with the apex entire, slightly bidentate, or irregularly dentate; nerves of the lemma not prolonged beyond the apex; lemma muticous or with a short subapical awn (but awned in *T. filifolium* var. *aristatum*).

2a. Glumes very unequal in length, shorter than the spikelet, covering nearly half of the spikelet length; spikelets 1- to 3-flowered; lemma with the apex obtuse to irregularly dentate; leaf blades flat or sometimes convolute or involute, never filiform; lodicules lanceolate, acute at the apex.
3a. Panicles 4–12 cm wide, open, lax; the branches capillary and flexuous; first glume 1.4–2.6 mm long; second glume 2–4.5 mm long ..... 5. *T. pringlei*
3b. Panicles 0.6–1 cm wide, narrow and densely flowered; the branches closely appressed; first glume (2.7–)3–4 mm long; second glume 4–5.8 mm long ..... 1. *T. angustum*
2b. Glumes subequal to equal in length, about two-thirds as long as the spikelet or as long as the spikelet; spikelets 2- or 3-flowered; lemma with the apex slightly bidentate to entire; leaf blades involute, filiform; lodicules linear, slightly bilobate at the apex.
4a. Lemma muticous or with a short subapical mucro 0.2–0.5 mm long 3a. *T. filifolium* var. *filifolium*
4b. Lemma awned on the upper third; the awn 3–5 mm long, geniculate ..... 3b. *T. filifolium* var. *aristatum*
1b. Lemmas bidentate at the apex; intermediate and marginal nerves or only intermediate nerves prolonged beyond the apex as 2 to 4 apical setae; apical teeth sometimes without nerves; lemma aristate, the awn well developed, borne on the upper third, middle, or lower third of the lemma, not subapical.
5a. Awn always inserted on the upper third of the lemma (sometimes nearly in this position in *T. palmeri*); glumes unequal, the first glume shorter and narrower than the second glume; apex of the lemma with two setae formed by the projection of the intermediate nerves; lemma ± keeled in cross section; palea gaping (*Trisetum* subg. *Trisetum*).
6a. Panicles 2–15 cm wide, lax, mostly open or narrow, pyramidal; ovary pubescent or glabrous; culms glabrous below the inflorescence (*Trisetum* sect. *Trisetum*).
7a. Lemmas (2.5–)2.7–4.3 mm long, smooth to slightly scabrous; apex of the lemma bidentate; dorsal awn delicate, curved; first glume 1.7–2.5 mm long; second glume 2.8–3.8 mm long; lodicules truncate at the apex; endemic to Nuevo León, Mexico ..... 2. *T. currisetum*
7b. Lemmas 4.3–6 mm long, strongly scabrous; apex of the lemma biaristulate; dorsal awn not delicate, geniculate; first glume 2.5–5 mm long; second glume 3.5–6.5 mm long; lodicules lobulate at the apex; from central Mexico to Peru ..... 4. *T. irazuense*
6b. Panicles 0.5–1.3(–2) cm wide, spiciform or subspiciform; ovary glabrous; culms pubescent below the inflorescence.
8a. Lemmas glabrous; glumes scabrous on the keel, not ciliate; awn slightly scabrous; paleas scabrous on the keels (*Trisetum* sect. *Trisetaera*).
9a. Glumes shorter than the spikelet, wide, the first 1-nerved, the second 3-nerved; ligule 0.5–1 mm long; plant not rhizomatous ..... 9. *T. spicatum*
9b. Glumes as long as the spikelet, the first (1)3-nerved, the second (3)5-nerved; ligule 3–4 mm long; plants rhizomatous ..... 7. *T. ligulatum*
8b. Lemmas pubescent; glumes scabrous or ciliate on the keel; awn scabrous or plumose; paleas scabrous or ciliate on the keels.
10a. Glumes ciliate on the keel and slightly shorter to as long as or longer than the spikelet; first glume 3.7–6 mm long, ovate-lanceolate; second glume 4.5–6.5 mm long, ovate-lanceolate to ovate; lemma awns plumose; paleas ciliate on the keels ..... 8. *T. rosei*
10b. Glumes somewhat scabrous on the keel and shorter than the spikelet (about ⅔ the length); first glume 3–3.2 mm long, linear-lanceolate; second glume about 4 mm long, linear-lanceolate to lanceolate; lemma awns not plumose, but ciliate near the base; paleas scabrous on the keels ..... 6. *T. barbatipaleum*
5b. Awn inserted on the lower third or near the middle of the lemma; glumes subequal, nearly as long as the spikelet or longer; lemma with apical teeth without prolongation of the intermediate nerves or with 2 to 4 setae; lemma rounded in cross section; palea sometimes enclosed by the margins of the lemma, not gaping (*Trisetum* subg. *Deschampsioidea*).
11a. Spikelets 2-flowered; panicles narrow, subspiciform to spiciform, 0.6–2(4) cm wide.
12a. Glumes equal in length and longer than the spikelet; spikelets 7.5–9 mm long; lemmas bidentate at the apex; panicles 1.5–2(–4) cm wide, tinged with purple and gold; ovary with trichomes at the apex ..... 11. *T. martha-gonzaleziae*
12b. Glumes subequal, shorter than the spikelet; spikelets 6.5–7 mm long; lemmas with four setae at the apex; panicles 0.6–1 cm wide, green; ovary glabrous at the apex 13. *T. pinetorum*
11b. Spikelets 2- to 6-flowered; panicles open, lax, (1–)2–20 cm wide.
13a. Culms 150–300 cm tall, bambusiform, 5–7(–10) mm diam. below; lemma apex 2- or 4-dentate or -toothed, sometimes appearing almost entire, the lateral nerves do not contain nerves (vascular tissue) ..... 17. *T. virletii*
13b. Culms 40–150 cm tall, herbaceous, usually less than 4 mm diam. below; lemma apex 2-lobed, or 4-awned due to the projection of intermediate and marginal nerves (setae) beyond the apex.
14a. Lemmas dorsally hirsute below the awn insertion; ovary with trichomes at the apex 10. *T. durangense*
14b. Lemmas glabrous or dorsally scabrous; ovary glabrous, rarely pilose (see *T. martha-gonzaleziae*).

15a. Lemma apex 2-lobed and 4-awned as teeth or setae.
16a. Lemmatal awns borne above the middle of the lemma.
17a. Lemma apex with four setae, the setae 0.6–1 mm long; paleas slightly shorter than the lemma; callus trichomes 1.2–1.7 mm long ..... 15. *T. tonduzii*
17b. Lemma apex without four setae; paleas as long as or slightly longer than the lemma; callus trichomes 0.5–1 mm long or less ..... 12. *T. palmeri*
16b. Lemmatal awns borne near the middle or on lower ⅓ or ¼ of the lemma.
18a. Ligules 3–6 mm long; paleas as long as or slightly longer than the lemma; rachilla trichomes about 0.5–1(–1.4) mm long ... 12. *T. palmeri*
18b. Ligules 0.5–1(–2) mm long; paleas shorter than the lemma; rachilla trichomes 1.5–3 mm long ..... 16. *T. viride*
15b. Lemma apex 2-lobed without any additional awns or setae.
19a. Spikelets (4)5- to 6-flowered ..... 14. *T. spellenbergii*
19b. Spikelets 2- or 3-flowered.
20a. Ligules 3–6 mm long; rachilla trichomes 0.5–1(–1.4) mm long ..... 12. *T. palmeri*
20b. Ligules 0.5–1(–2) mm long; rachilla trichomes 1.5–3 mm long.
21a. Glumes 7.5–9 mm long, equal, longer than the spikelet; panicles 1.5–2(–4) cm wide, contracted, subspiciform; ovary pilose ..... 11. *T. martha-gonzaleziae*
21b. Glumes 3–7 mm long, unequal, shorter than the spikelet; panicles 2–8 cm wide, open or somewhat contracted; ovary glabrous ..... 16. *T. viride*

1. **Trisetum angustum** Swallen, Phytologia 4(7): 423. 1953. TYPE: Guatemala. San Marcos: between San Sebastián and summit of Volcán Tajumulco, on top of dry ridge in pine forest, 13 Feb. 1940, *J. A. Steyermark 35525* (holotype, F-1046546!; isotype, US-2236479 fragment & photo ex F!).

Perennial; culms 12–24 cm tall, glabrous, densely caespitose. Leaf sheaths glabrous or pubescent below; ligule 1.5–2.2 mm long; blades 3–8 cm × ca. 1 mm, flat, glabrous or sparsely pilose. Panicles 4–11 × 0.6–1 cm, narrow, densely flowered, the branches closely appressed. Spikelets 4.6–6 mm long, 2-flowered; rachilla sparsely pubescent, the trichomes about 0.6 mm long; glumes shorter than the spikelet, unequal; first glume (2.7–)3–4 mm long, 1-nerved; the second glume 4–5.8 mm long, 3-nerved; lemmas (lowest) 4–4.8 mm long, scabrous; apex irregularly toothed to 4-dentate, muticous or with a short subapical mucro; the mucro up to 0.5 mm long; callus obtuse, short pubescent, the trichomes 0.2–0.6 mm long; anthers 0.8–0.9 mm long. Caryopses ca. 2.1 mm long; endosperm solid, hard.

Distribution. This species was described from a Guatemalan specimen by Swallen (1953). A specimen from Chiapas, Mexico (*Matuda 2342a*), was cited in Pohl and Davidse (1994); however, we were not able to study this. This species was not cited for Mexico by Hernández-Torres and Koch (1988) but was included in Espejo-Serna et al. (2000).

Comments. The above description is based on the study of type material and includes the description for *Trisetum angustum* given by Pohl and Davidse (1994), who also studied the holotype. This species appears closely related to *T. pringlei*. Pohl and Davidse (1994) suggested that *T. angustum* might be better treated as a variety of *T. pringlei* since these species are morphologically very similar. Both species have obtuse lemma apices and lack well-developed awns. These characteristics do not correspond well with the generic characteristics of *Trisetum*. Therefore, we consider the systematic position of these two species to be tentative or provisional. We have placed *T. angustum* and *T. pringlei* in *Trisetum* subg. *Trisetum* but have not assigned them to a section (see Appendix 1).

2. **Trisetum curvisetum** Morden & Valdés-Reyna, Brittonia 35: 375. 1983. TYPE: Mexico. Nuevo León: Zaragoza, Sierra Madre Oriental, Ejido La Encantada, sitio La Tinaja, 1 km N del aserradero, ca. 23°55′N, 99°45′W, 2830 m, 25 July 1981, *Valdés-Reyna & Capó VR-1419* (holotype, TAES not seen; isotypes, ANSM not seen, ENCB not seen, MEXU not seen, MO-3102085 not seen, NY not seen, TEX not seen, US-2978399!, UT not seen, XALU not seen).

Perennial, with short rhizomes; culms 50–150 cm tall, glabrous, weak; nodes 4, glabrous, dark. Leaf sheaths shorter than the internodes, glabrous to sparsely pubescent or only ciliate on the margins; ligule 1.1–2.5 mm long, membranous, oval,

ciliate or denticulate; blades (5–)9–20 cm × 1.5–8.5 mm, flat, glabrous or sparsely pubescent on the adaxial surface. Panicles 11–30(–36) × 2–15 cm, lax, mostly open, pyramidal, paucispiculate, rachis glabrous; pedicels 0.5–4.5 mm long, scabrous toward the apex; the branches flexuous, in verticels of five, ascending, widely spaced below becoming crowded near the apex. Spikelets 3–5.2 mm long, (1)2- or 3-flowered; rachilla 1–1.8 mm, glabrous to scabrous, sometimes with a few trichomes at the apex; glumes shorter than the spikelet, unequal, margins hyaline, apex acute, scabrous on the keel; first glume 1.7–2.5 mm long, linear-lanceolate, attenuate, 1-nerved; second glume 2.8–3.8 mm long, ovate-lanceolate, 3-nerved; lemmas (2.5–)2.7–4.3 mm long, lanceolate, laterally compressed, slightly keeled, awned, 5-nerved, the nerves conspicuous, glabrous to scabrous, slightly bidentate at the apex or the apex entire, the margins and apex hyaline; awn 3–5.5 mm long, borne on the upper ¼ or ⅕, less than 1 mm from the apex, flexuous, delicate, curved, scabrous; callus obtuse, glabrous or sparsely pubescent, the trichomes ca. 0.1 mm long; paleas 2–3.1 mm long, hyaline, shorter than the lemma, 2-nerved, the nerves scabrous, acute at the apex; lodicules oblong truncate, 0.2–0.3 mm long; anthers 0.5–1 mm long; ovary with 1 or 2 short, curved and shining trichomes on the apex. Caryopses 1.7–2.2 × 0.4–0.6 mm; endosperm soft.

Chromosome number. $2n = 28$ (Hernández-Torres & Koch, 1988).

Anatomy and micromorphology. Ligule apices composed of papillose cells; trichomes absent; ligule epidermis more or less rectangular, short, with straight walls; prickles and macrohairs absent. Leaf sections flat; keeled and well developed; adaxial ribs absent; bulliform cells in fan-shaped groups between vascular bundles; abaxial epidermis composed of fusiform long cells, with straight walls; prickles present; short cells present both in costal and intercostal zones; stomata present only in abaxial epidermis.

Distribution. Endemic to Mexico, known only from Nuevo León, 2100–2500 m.

Comments. Although the occurrence of oblong truncate lodicules in *Trisetum curvisetum* is unusual in the genus in comparison with the typical form (lobulate to irregularly lobed or toothed) in the genus (Morden & Valdés-Reyna, 1983), no other characters seem to pose questions as to the generic position of this species. The presence of short, curved, and shining trichomes on the apex of the ovary and caryopsis confirms its generic position. The habit of the plant, the structure of the panicle, the morphology of the spikelets, the presence of trichomes on the ovary, and caryopsis shape all suggest an affinity with *T. cernuum*.

Specimens studied. MEXICO. **Nuevo León:** Zaragoza, Sierra Madre Oriental, 7 km SE antes de La Encantada, por el camino Zaragoza–Ejido La Encantada, 23°55′N, 99°45′W, 25 July 1981. *J. Valdés-Reyna & M. Capó VR-1417* (US-2978400, paratype); ca. 15 mi. SW of Aramberri, 24°02′32.2″N, 99°44′04.1″W, 20 Sep. 2002, *Peterson et al. 16719* (ANSM, CONC, US); ca. 17 mi. SW of Aramberri, 20 Sep. 2002, *Peterson et al. 16723* (ANSM, CONC, US); Sitio La Encantada-La Tinaja on road to La Tinaja, 23°53′14.4″N, 99°47′44.2″W, 21 Sep. 2002, *Peterson et al. 16764* (ANSM, CONC, US).

3a. Trisetum filifolium Scribn. ex Beal var. **filifolium,** Grasses N. Amer. 2: 375. 1896. TYPE: Mexico. Chihuahua: cool slopes of the Sierra Madre, 9000 ft., 3 Oct. 1887, *C. G. Pringle 1431* (holotype, US-81773!; isotypes, CM not seen, US-825600!).

Perennial, caespitose, rhizomes absent; culms 30–60 cm tall, glabrous. Leaf sheaths glabrous, scaberulous, or pubescent; ligule (0.2–)1–3.5 mm long, membranous, truncate, glabrous or with short trichomes; blades 5–22 cm × 0.5–2 mm, involute, filiform, curved and flexuous, glabrous or slightly scabrous. Panicles 12–15 × 2–3 cm, lax, somewhat open, narrow, exserted; the branches semiverticillate, the half-whorls with 3 to 7(8) branches, the lower ones 4–6 cm long; rachis glabrous. Spikelets 3.5–6 mm long, (1)2- or 3-flowered; pedicels scabrous; rachilla 1–1.2 mm long, with trichomes ca. 1.5 mm long, the trichomes longer at the apex; glumes subequal, shorter, slightly longer, or about as long as the spikelet; first glume 2.5–6 mm long, 1(3)-nerved, second glume 3–7 mm long, 3-nerved; lower floret 3.5 mm long; lemmas 3.5–5 mm long, obscurely 5-nerved, strongly scabrous, sometimes scabrous-pubescent, terete, the margins involute enclosing the palea; apex entire or shortly bilobed, each lobe with two short teeth, muticous or with a short subapical mucro; mucro 0.2–0.5 mm long; callus pubescent or subglabrous, obtuse, trichomes ca. 0.2 mm long; paleas 3–4.5 mm long, shorter than the lemma, enclosed by the involute margins of the lemma (not gaping), 2-keeled, the keels well apart, ciliate or conspicuously scabrous; lodicules with acute apex and a lateral lobe below the middle, 0.4–0.5 mm long; anthers 1–2 mm long; ovary glabrous. Caryopses 1.5–2 mm long; endosperm solid.

Anatomy. Leaf blades in transverse section are without a well-developed keel and with prominent ribs; furrows more than one half of the leaf thick-

ness; sclerenchyma present as a continuous abaxial band, adaxial girders T-shaped, marginal sclerenchyma present; adaxial epidermis has trichomes and inconspicuous bulliform cells; the abaxial epidermis lacks trichomes or prickles.

Distribution. Endemic to Chihuahua, Durango (Herrera-Arrieta, 2001), and Hidalgo, Mexico, 1600–3100 m.

Comments. *Trisetum filifolium* differs from typical *Trisetum* species by having a terete lemma (vs. lemma keeled), the lemma apex entire or bilobed (vs. 2-aristulate to 2-dentate in *Trisetum*), the palea enclosed by the lemma (free from the lemma in *Trisetum*), and by having linear lodicules (vs. 2 or 3 lobate at the apex in *Trisetum*).

Specimens studied. MEXICO. **Chihuahua:** Sánchez, 12 Oct. 1910, *Hitchcock 7682* (US); 27.6 mi. NW of Rocheachi on road to Basigochi, 19 Sep. 1991, *Peterson et al. 10797* (US). **Hidalgo:** Zacualtiplán, trailside, slopes & ravines by Río Panotlán, between Zacualtiplán & Olotla on road to Metztitlán, 3 July 1947, *Moore 3250* (US).

KEY TO VARIETIES OF *TRISETUM FILIFOLIUM*

1a. Lemmas mucronate, the mucro 0.2–5 mm long, inserted apically ..... 3a. *T. filifolium* var. *filifolium*

1b. Lemmas awned, the awn 3–5 mm long, geniculate and twisted, borne on the upper third of the lemma, i.e., inserted below the apex ..... 3b. *T. filifolium* var. *aristatum*

3b. Trisetum filifolium var. **aristatum** Scribn. ex Beal, Grass. N. Amer. 2: 375. 1896. TYPE: Mexico. Chihuahua: cool slopes of the Sierra Madre, alt. 9000 ft., 7 Oct. 1887, *C. G. Pringle 1430* (holotype, US-868411!; isotypes, MO-3727972 not seen, NY not seen).

Distribution. Endemic to Mexico in the Sierra Madre Occidental in Chihuahua and Durango and Sierra Madre Oriental in Coahuila, México, and Hidalgo (Hernández-Torres & Koch, 1988; Finot, 2003b).

Comments. Though Beal (1896) suggested that variety *aristatum* could be a different species, the overall morphology of the plant and the structure of the spikelets conform with the general description of *Trisetum filifolium*.

Specimens studied. MEXICO. **Durango:** 3.2 mi. S of La Peña on road toward La Puerta, 15 Sep. 2003, *Peterson et al. 17785* (CIIDIR, US). **Hildalgo:** Zimapán, near Puerto Ing. Isidro Díaz, km 230–235 on hwy. between Zimapán & Jacala, 7 July 1948, *Moore & Wood, Jr. 3765* (US). **México:** 28.3 mi. NE of Temascaltepec on Mex 134 towards Toluca, 7 Oct. 1991, *Peterson & Annable 11084* (US).

4. Trisetum irazuense (Kuntze) Hitchc., Proc. Biol. Soc. Wash. 40: 82. 1927. Basionym: *Calamagrostis irazuensis* Kuntze, Revis. Gen. Pl. 2: 763. 1891. TYPE: Costa Rica. Volcán Irazú, 3000 m, Waldregion, 24 June 1874, *C. E. O. Kuntze 2334* (holotype, NY-346300 ex Herb. Kuntze!).

Trisetum scabriflorum Hitchc., Contr. U.S. Natl. Herb. 24: 358, 1927. TYPE: Colombia. Cauca: collected below Pitayó, Río Palo Basin, Tierra Adentro, 2400 m, Feb. 1906, *H. Pittier 1435* (holotype, US-531631!).

Trisetum scabrivalve Sodiro, Revista Colegio Nac. Vicente Rocafuerte 11: 84, 88 (Reprint 32, 36), 1930. TYPE: Ecuador. Crece en los pajonales del Pichincha, Paluguillo (Pifo), Chimborazo y El Altar (type not located).

Trisetum gracile E. Fourn., Mexic. Pl. 2: 108. 1886, hom. illeg., non *Trisetum gracile* (Moris) Boiss. *Trisetum fournieranum* Hitchc., Contr. U.S. Natl. Herb. 17: 326. 1913. TYPE: "San Luis de Potosí," *M. Virlet d'Aoust 1382* (lectotype, designated here, P!; isotype, US-726971b fragment ex P!).

Perennial, caespitose; culms 75–100 cm tall, glabrous, up to 2 mm diam. on the lower internodes; nodes 3, glabrous. Leaf sheaths shorter or slightly longer than the internodes, glabrous or pubescent; basal sheaths pubescent; ligule 2–4 mm long, membranous, pubescent to densely pubescent, the apex truncate, dentate or ciliate; blades 20–30 cm × 2.5–6 mm, flat, glabrous or pubescent; upper blades 5–10 cm long. Panicles (7–)13–25 × (1–)2–5 cm wide, lax, narrow, yellow-green to deep green and purple; rachis glabrous to sparsely pubescent; the branches appressed and ascending. Spikelets 4–7(–9) mm long, 2- or 3-flowered; pedicels 2–7 mm long, glabrous to sparsely pubescent, sometimes scabrous; rachilla 1–1.7 mm long, covered with stiff trichomes, the trichomes 0.5–1 mm long; glumes very unequal, shorter than the spikelet; the keel scabrous on the upper half, the margins hyaline; lower glume 2.5–5 mm long, narrow, linear, 1-nerved, acute at the apex, half as long as the spikelet; upper glume 3.5–6.5 mm long, lanceolate to ovate-lanceolate, abruptly attenuate, 3-nerved, ¾ as long as the spikelet; lemmas 4.3–6 mm long, 5-nerved, the nerves inconspicuous toward the base, strongly scabrous on the upper half, green and purplish toward the apex, sometimes with short trichomes toward the base; apex awned, hyaline, biaristate or toothed, the apical awns ca. 0.5 mm long, conspicuous; awn (2.5–)5.5–8.5 mm long, borne on the upper ⅓ or ¼, straight or twisted and geniculate; callus obtuse, with short trichomes, the trichomes ca. 0.2–0.3 mm long; paleas 3.2–4.6 mm long, slightly shorter than the lemma, hyaline, 2-keeled, the keels scabrous on the upper half, 2-dentate to 2-awned at the apex; lodicules ca. 0.7

mm long, bilobed at the apex, the lobes acute; anthers (0.8–)1.2–1.8 mm long; ovary glabrous. Caryopses 2.2–3 mm long; endosperm soft.

Chromosome numbers. $2n = 28, 42$ (Hernández-Torres & Koch, 1988).

Anatomy. Leaf blades are flat in transverse section, with rounded adaxial ribs; furrows less than one half of the leaf thickness; first-order vascular bundles with adaxial and abaxial girders; second-order vascular bundles with adaxial girder; third-order vascular bundles with small sclerenchyma strands; bulliform cells in fan-shaped groups at the base of the furrows; abaxial epidermis with fusiform intercostal long cells with straight side walls; stomata not seen; prickles rare; trichomes present; costal cork cells and silica bodies in pairs or short rows.

Distribution. This species has been reported for Mexico (Chiapas, Distrito Federal, Durango, Hidalgo, México, Oaxaca, Puebla, San Luis Potosí, and Veracruz), Costa Rica, Panama, Honduras, Colombia, Venezuela, Ecuador, and Peru; 2700–3600 m (Pohl, 1980; Hernández–Torres & Koch, 1988; Davidse et al., 1994; Finot, 2003b).

Comments. A lectotype (*M. Virlet d'Aoust 1382*) at P was here chosen to stabilize the name since there was another syntype (*F. M. Liebmann 613*) cited in the original protologue by Fournier (1886). A specimen of *Liebmann 613* was not found at P.

Specimens studied. COSTA RICA. **San José:** pasture upper slopes of volcán Irazú, 24 Feb. 1965, *Godfrey 66635* (US); San José, S-SW of Cerro Chirripó, 10 Dec. 1967, *Weston 3673* (CR). GUATEMALA. **Huehuetenango:** near Tunimá, Sierra de los Cuchumatanes, 6 July 1942, *Steyermark 48276* (US 2208636). MEXICO. La Hoya, *Liebmann 613* (isosyntypes, C, US-726971). **México:** Popo Park, 1 Aug. 1910, *Hitchcock 1448* (P), 4–8 Aug. 1910, *Hitchcock 5974* (US); open fir woods, Sierra de Las Cruces, 5 Oct. 1895, no collector (P). PANAMA. **Chiriquí:** Chiriquí volcano, 29 Sep. 1911, *Hitchcock 8221* (US), 29–30 Sep. 1911, *Hitchcock 8224* (S). PERU. **Piura:** 23 km E of Sóndor, on road toward Tabacones, 31 Mar. 2000, *Peterson & Refulio-Rodríguez 15135* (US).

5. Trisetum pringlei (Scribn. ex Beal) Hitchc., Proc. Biol. Soc. Wash. 40: 82. 1927. Basionym: *Graphephorum pringlei* Scribn. ex Beal, Grasses N. Amer. 2: 561. 1896. TYPE: Mexico. Oaxaca: summit of Sierra de San Felipe, 10,000 ft., 4 Aug. 1894, *C. G. Pringle 4765* (holotype, US-822340!; isotypes, CM not seen, ENCB not seen, MO not seen, P!, US-749287!, US-251958!).

Perennial, caespitose; culms 25–80 cm tall, glabrous; nodes (1)2 or 3, glabrous. Leaf sheaths glabrous or pubescent, sometimes only pubescent at the apex, shorter or longer than the internodes, sometimes one side extended above summit as a sheath auricle; ligule 0.5–1.5 mm long, the apex truncate to ovate, minutely denticulate and ciliate; blades 4–9(–12) cm × 2–5 mm, flat, sometimes subinvolute, the lower blades glabrous or pubescent, ciliate on the margins, the upper blades glabrous. Panicles 4–17 × 4–12 cm, open, lax, usually purplish; branches up to 8 cm long, verticillate, capillary and flexuous; rachis glabrous to somewhat scabrous. Spikelets 3.5–6.5 mm long, 1- or 2(3)-flowered, pedicels up to 4 mm long, capillary, glabrous, purple; rachilla 1–1.5 mm long, with trichomes 0.5–1 mm long, distributed toward the apex; glumes unequal, shorter than the spikelet, acute, the keel smooth or scabrous on the upper half; first glume 1.4–2.6 mm long, linear-lanceolate, shorter and narrower than the second, 1-nerved; second glume 2–4.5 mm long, lanceolate, 3-nerved; lemmas 2.6–4 mm long, strongly scabrous, sometimes covered by short trichomes, purple, terete, 5-nerved, the nerves conspicuous toward the apex; margins hyaline; apex truncate, entire or mucronate; subapical mucro when present less than 1 mm long; paleas 2.2–2.9 mm long, shorter than the lemma, hyaline, 2-nerved, sometimes purple-tinged, the keels scabrous to ciliate-scabrous on the upper half; callus obtuse, with trichomes 0.1–0.5 mm long; lodicules 0.4–0.7 mm long, linear, not lobed, the apex obtuse, ciliate; apex rounded or acute; anthers 0.6–1.2 mm long; ovary glabrous. Caryopses 1.4–1.9 mm long, ca. 0.4 mm wide; endosperm solid.

Anatomy and micromorphology. Leaf ligule apex has only papillate cells and the epidermis is composed of more or less rectangular long cells with straight side walls; hooks and prickle hairs present; stomata were not seen. Leaf blades in transverse section are without a keel and have well-developed ribs; furrows more than one half of the leaf thickness, bulliform cells inconspicuous; vascular bundles with both adaxial and abaxial girders alternate with free bundles without associated sclerenchyma, adaxial girder T-shaped, abaxial girders I-shaped, marginal sclerenchyma present; trichomes on both adaxial and abaxial surfaces, stomata present on the adaxial epidermis; abaxial epidermis composed of long cells with undulate side walls; costal cork cells-silica bodies present, trichomes present, prickles not seen.

Distribution. Mexico (Chiapas, Oaxaca, Puebla), Guatemala, Costa Rica, and Panama; 1500–3500 m (Hernández-Torres & Koch, 1988; Finot, 2003b).

Comments. The number of florets in *Trisetum pringlei* varies from one to three per spikelet. One-flowered spikelets are infrequent in *Trisetum*, and are found in some individuals of *T. filifolium*, *T. pringlei*, and in the South American *T. ambiguum* Rúgolo & Nicora (Rúgolo de Agrasar & Nicora, 1988).

On the basis of morphological, anatomical, and embryological characteristics, Hernández-Torres and Koch (1988) concluded that this species belongs in *Trisetum*, as was proposed by Hitchcock (1927). *Trisetum pringlei* differs from typical species of *Trisetum* by having lemma apices that are entire and mucronate, and linear lodicules with entire (not lobed) apices. Further studies are needed to clarify the generic assignment of *T. pringlei* (see Appendix 1).

Specimens studied. COSTA RICA. **Cartago:** along the Pan American Hwy., Cerro de la Muerte, 8 Aug. 1972, *Taylor 11750* (US); Cráter volcán Irazú, 26 Oct. 1950, *Anderson 1339* (US-2042177); Cerro de la Muerte, Pan American Hwy., 5 km above Millsville, cordillera de Talamanca, 22 July 1949, *Holm & Iltis 483* (P). **San José:** Cordillera de Talamanca, Cerro de La Muerte, Asunción summit, 13 July 1968, *Pohl & Davidse 10694* (CR). GUATEMALA. **Huehuetenango:** between Tojquiá and Caxín bluff, summit of Sierra de los Cuchumatanes, 6 Aug. 1942, *Steyermark 50224* (US). **Totonicapán:** region of Chiu Jolán, mounts above Totonicapán, on road to Desconsuelo, 23 Jan. 1941, *Standley 84473* (US). PANAMA. **Chiriquí:** Chiriquí Volcano, 29–30 Sep. 1911, *Hitchcock 8228* (US). MEXICO. **Oaxaca:** summit of Sierra de San Felipe, 4 Aug. 1894, *Pringle 4756* (P); vicinity of Cerro San Felipe, 1894, *Nelson 1108* (US).

6. Trisetum barbatipaleum (Hultén ex Veldkamp) Finot, Contr. U.S. Natl. Herb. 48: 661. 2003. Basionym: *Trisetum spicatum* var. *barbatipaleum* Hultén ex Veldkamp, Gard. Bull. Singapore 36(1): 135. 1983. *Trisetum spicatum* subsp. *tolucense* var. *barbatipaleum* Hultén, Svensk Bot. Tidskr. 53: 223. 1959, nom. inval. TYPE: Mexico. Hidalgo: Trinidad Iron Works, 1770 m, 21 Aug. 1905, *C. G. Pringle 10032* (lectotype, designated by Veldkamp, in Veldkamp & Van der Have (1983: 135), S not seen; isotypes, C not seen, L not seen, P!, SI!, US-462083!).

Perennial, caespitose; culms ca. 40 cm tall, pubescent; nodes pubescent. Leaf sheaths shorter than the internodes, pubescent; blades ca. 7 cm × 1–2 mm, flat, pubescent abaxially, glabrous adaxially. Panicles 8–10 × 0.5–1 cm, spiciform, interrupted; rachis pubescent; pedicels pubescent. Spikelets 5–5.2 mm long, 2-flowered; rachilla ca. 1 mm long, pilose; glumes unequal, shorter than the spikelet, somewhat scabrous on the keel; first glume 3–3.2 mm long, shorter and narrower than the second glume, linear-lanceolate to lanceolate, slightly longer than half of the spikelet, 1-nerved; second glume ca. 4 mm long, ovate-lanceolate to ovate, ⅔ as long as the spikelet, 3-nerved; lemmas 3.5–5 mm long, pubescent, 2-aristulate at the apex, awned on the upper third; awn ca. 6 mm long, curved, divaricate, not geniculate or twisted, ciliate near the base and scabrous above; callus with short trichomes, the trichomes ca. 2 mm long; paleas shorter than the lemma, ciliate toward the apex. Lodicules ca. 1 mm long, bilobed at the apex; ovary glabrous. Caryopses not seen.

Distribution. Endemic to Mexico where the species is known only from the type locality.

Comments. *Trisetum barbatipaleum* differs from *T. spicatum* in having conspicuously pubescent lemmas. It is closely related to *T. rosei* and differs from the latter by having a narrower panicle, glumes that are shorter than the spikelets and scabrous along the keel, and a first glume that is narrow and linear-lanceolate. *Trisetum rosei* has ovate glumes as long as the spikelet, a wider and more densely flowered panicle, glumes that are conspicuously ciliate on the keel, and a lemma with a plumose awn.

7. Trisetum ligulatum Finot & Zuloaga, sp. nov. TYPE: Mexico. Veracruz: La Perla, N side of Pico de Orizaba, above the Piedra Grande mountaineering shelter, 19°03′N, 97°16′W, 4200 m, 21 Sep. 1986, *M. Nee 33192* (holotype, SI!; isotype, CONC!). Figure 1.

Planta rhizomatosa, 13–30 cm alta; culmi erecti, pilosi; vaginae pilosae; ligula 3–4 mm longa, hialina, truncata, dorso pilosa; laminae planae (5–20 cm × 1–2.5 mm), pilosae; panicula spiciformis; spicula 5–6.5 mm longa, 2–3-flora; glumae subaequales, inferiores (1)3-nervatae, superiores (3)5-nervatae; lemmata scabra, 5-nervata, ad terciam superiorem aristata, apice biaristato; arista 2–3.5 mm longa; callus breve pilosus; palea paulo brevior quam lemma; lodiculae ad apicem 3-lobatae; ovarium glabrum.

Perennial, with short rhizomes; culms 13–30 cm tall, erect, pilose below the panicle, the trichomes antrorse above then retrorse below; nodes 1 to 3, glabrous. Leaf sheaths longer than the internodes, pubescent; ligules 3–4 mm long, dorsally pilose, truncate; blades 5–20 cm × 1–2.5 mm, flat or conduplicate, pubescent. Panicles 5–9 × 0.5–1.2 cm, spiciform, green or purple; rachis densely pubescent; spikelets 5–6.5 mm long, 2- or 3-flowered; rachilla ca. 1 mm long, sparsely pubescent, the trichomes 0.5 mm long; glumes subequal, nearly as long as the spikelet, acute, the keel scabrous on the upper half, green or purple; first glume 3.8–6

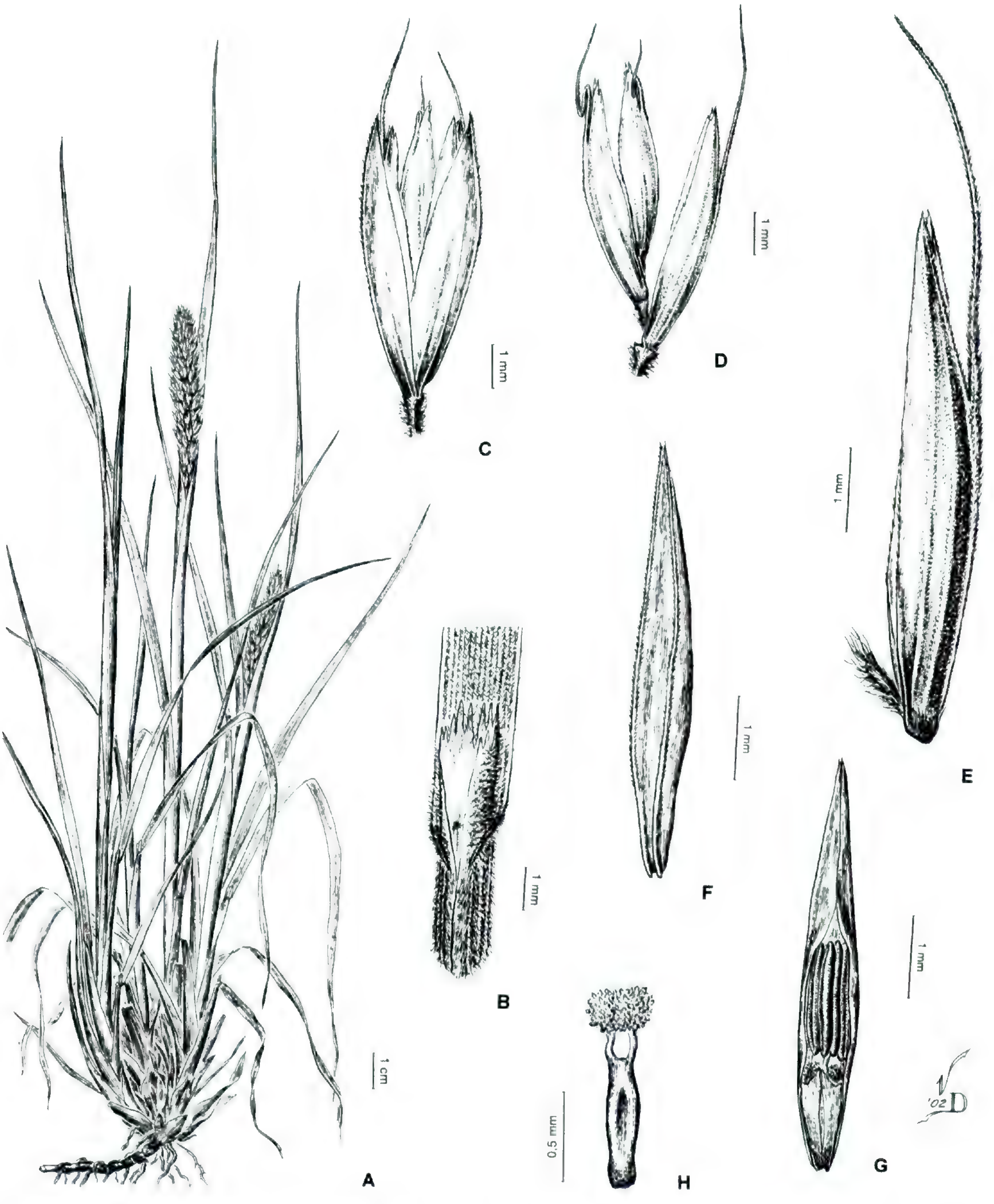

Figure 1. *Trisetum ligulatum* (*Nee 33192*). —A. Habit. —B. Sheath, ligule, and portion of the blade. —C. Spikelet. —D. Florets (3). —E. Floret. —F. Palea, dorsal view. —G. Palea, lodicules, and stamens, ventral view. —H. Pistil.

mm long, as long as or shorter than the first floret, (1)3-nerved; second glume 4.5–6.5 mm long, (3)5-nerved; lemmas 4.3–6.5 mm long, scabrous, 5-nerved, keeled, awned; margins hyaline toward the apex; apex biaristate; awn inserted on the upper third, 2–3.5 mm long, curved, scabrous; callus short pilose, the trichomes 0.5 mm long; palea nearly as long as its lemma, scabrous on the keels; lodicules 3-lobed at the apex; anthers ca. 1.5 mm; ovary glabrous. Caryopses not seen.

Anatomy. Leaf blades in transverse section are without a keel and have well-developed ribs with furrows more than half the leaf thickness; bulliform

cells are inconspicuous, trichomes present only in the abaxial epidermis, continuous abaxial sclerenchyma band absent, vascular bundles of first order without girders, bearing small strands of both adaxial and abaxial sclerenchyma, marginal sclerenchyma present; stomata present in both adaxial and abaxial epidermes; abaxial epidermis with rectangular to fusiform long intercostal cells, short costal cells solitary or in cork cell-silica body pairs, prickle hairs present.

Distribution. This new species is known only from the higher elevations (3810–4200 m) of Jalisco and Veracruz, Mexico.

Comments. *Trisetum ligulatum* resembles *T. spicatum* in having spiciform panicles and culms pilose below the inflorescence. It differs from *T. spicatum* in having short rhizomes (vs. none), dorsally pubescent ligules 3–4 mm long (vs. glabrous ligules ca. 1 mm long), spikelets with the first glume 3-nerved and the second glume 5-nerved (vs. first glume 1-nerved and second glume 3-nerved, and with both glumes nearly as long as the spikelet (vs. shorter than the spikelet).

Paratype. MEXICO. **Jalisco:** Nevado de Colima, 20 mi. SW of Ciudad Guzmán and 14 mi. SW of paved hwy. up road toward the Nevado, 23 Nov. 1995, *P. M. Peterson & R. Blackburn 13778* (US).

8. Trisetum rosei Scribn. & Merr., Contr. U.S. Natl. Herb. 8(4): 289. 1905. *Trisetum rosei* var. *tenerum* Scribn. & Merr., Contr. U.S. Natl. Herb. 8: 289. 1905. *Trisetum rosei* Scribn. & Merr. fo. *tenerum* (Scribn. & Merr.) Louis-Marie, Rhodora 30: 239. 1929. TYPE: Mexico. Volcán Popocatepetl, 3600 m, 7–8 Aug. 1901, *J. N. Rose & R. Hay 6016* (holotype, US-395813!; isotypes, ENCB not seen, MEXU-4703 not seen, NY-431715 not seen).

Perennial, caespitose; culms 25–50 cm tall, densely pubescent, the trichomes antrorse above then retrorse below; nodes 2. Leaf sheaths glabrous or retrorsely tomentose, shorter than the internodes; ligule 1–2.5 mm long, scabrous on the dorsal surface, truncate, conspicuously ciliate; blades 6–15 cm × 2–4 mm, flat, glabrous to pubescent on both sides, soft or stiff, conduplicate or the margins involute, the uppermost leaf blade 3–6 cm long. Panicles 6–13 × 1–1.5 cm, subspiciform, dense, ± linear, acute at the apex, sometimes interrupted; rachis pubescent. Spikelets 5–7 mm long, 2(3)-flowered; pedicels up to 3 mm long; rachilla ca. 1 mm long, pubescent, the trichomes stiff, ca. 0.5 mm long; glumes slightly shorter to as long as or longer than the spikelet, ciliate on the keel, the margin hyaline, the apex acute, faintly tinged with purple; first glume 3.7–6 mm long, lanceolate to ovate-lanceolate, usually 1- or 3-nerved; second glume 4.6–6.5 mm long, ovate-lanceolate to ovate, 3-nerved; lemmas 4.2–6.2 mm long, pubescent, awned; apex bisetulate and hyaline, seta 0.3–0.7 mm long; awn 2.5–5 mm long, borne on the upper third, plumose, curved, not twisted or bent; callus obtuse, with trichomes 0.3–0.5 mm long; paleas 3–4.5 mm long, glabrous to pubescent, shorter than the lemma, 2-nerved, the keels ciliate; apex bidentate, hyaline; lodicules 0.5–1 mm long, 2-lobed at the apex, the lobes unequal, acute; anthers 1–1.5 mm long; ovary glabrous. Caryopses 2.5–2.7 mm long, ca. 0.6 mm wide; endosperm liquid or soft.

Anatomy and micromorphology. Ligule apices have short stiff trichomes, and the epidermis is composed of more or less rectangular long cells with straight side walls, hooks very frequent; no trichomes or stomata were seen. Leaf blades in transverse section did not have a keel but had well-developed ribs with furrows more than one half the leaf thickness; bulliform cells inconspicuous; trichomes present in both adaxial and abaxial epidermes with a continuous abaxial sclerenchymatic band present; first- and second-order vascular bundles with adaxial and abaxial girders; adaxial girders T- or anchor-shaped; marginal sclerenchyma present; abaxial epidermis with long cells with undulated side walls, intercostal hooks and stomata present, cork cells and silica bodies present in costal zones; no trichomes were seen in the abaxial epidermis.

Distribution. Guatemala and Mexico (Hidalgo, México, Puebla, and Veracruz), between 2500 and 4300 m (Espejo-Serna et al., 2000).

Comments. *Trisetum rosei* was considered a synonym of *T. spicatum* by Hernández-Torres and Koch (1988). *Trisetum rosei* can be easily recognized by its pubescent lemmas, ciliate glumes, plumose awned lemmas, paleas with ciliate keels (vs. lemmas glabrous, glumes scabrous, lemma awns not plumose, and scabrous palea keels in *T. spicatum*), and, in cross section, an abaxial band of continuous sclerenchymatous tissue (absent in *T. spicatum*).

Specimens studied. GUATEMALA. **Huehuetenango:** Sierra de los Chuchumatanes, 6 July 1942, *Steyermark 48279* (US). MEXICO. **Hildalgo:** Inter Pachuca et Mineral del Chico, 20 Dec. 1931, *Fröderström & Hultén* 3 (S); mtns. above Pachuca, 4 Aug. 1898, *Pringle s.n.* (US); between Pachuca & Real del Monte, 19 July 1905, *J. N. Rose, Painter & J. S. Rose 8686* (US). **México:** Volcán Ixtaccihuatl, media falda, 13 Sep. 1953, *Matuda 29044* (US); 24.2 km E of Amecameca & 2.5 km S of Paso de

Cortéz, 10 Oct. 1991, *Peterson & Annable 11103* (US); Paso de Cortéz, 17 Sep. 1958, *Beaman 2562* (US); Mt. Popocatepetl, 5–6 Aug. 1910, *Hitchcock 5987* (US); Ixtaccihuatl, NW side of mt. ca. 9 km E of San Rafael, 16 July 1959, *Beaman 2853* (US). **Puebla:** N side of Popocatepetl, 11 Sep. 1957, *Beaman 1729a* (US); ca. 1 km Paso de Cortéz, 21 July 1959, *Beaman 2892* (US); Mt. Orizaba, 17–18 Aug. 1910, *Hitchcock 6261* (US); Mpio. San Nicolás de Los Ranchos, La Joya, Volcán Ixtaccihuatl, 7 km N carretera a Amecameca, 13 km E Amecameca, 28 Oct. 1976, *Koch 76231* (US); Mpio. de Tochimilco, Paso Cortéz, Tlamacos, 16 km ESE de Amecameca, 18 Oct. 1976, *Koch 76205b* (US). **Veracruz:** Mt. Orizaba, Mar. 1908, *Purpus 3018* (BAF); Pico de Orizaba, N of Cueva del Muerto, 21 Sep. 1957, *Beaman 1778a* (US).

9. Trisetum spicatum (L.) K. Richt., Pl. Eur. 1: 59. 1890. Basionym: *Aira spicata* L., Sp. Pl. 1: 64. 1753. *Aira subspicata* L., Syst. Nat. ed. 10 2: 873. 1759, nom. illeg. superfl. *Avena airoides* Koeler, Descr. Gram. 298. 1802, nom. illeg. superfl. *Trisetum subspicatum* (L.) P. Beauv., Ess. Agrost. 88, 149. 1812, nom. illeg. superfl. *Trisetaria airoides* (Koeler) Baumg., Enum. Stirp. Transsilv. 3: 265. 1816, nom. illeg. superfl. *Trisetum airoides* (Koeler) P. Beauv. ex Roem. & Schult., Syst. Veg. 2: 666. 1817, nom. illeg. superfl. *Koeleria subspicata* (L.) Rchb., Fl. Germ. Excurs. 49. 1830, nom. illeg. superfl. *Koeleria spicata* Rchb. ex Willk. & Lange, Prodr. Fl. Hispan. 1: 72. 1861, nom. inval. *Trisetaria spicata* (L.) Paunero, Anales Jard. Bot. Madrid 9: 516. 1959. TYPE: Sweden. Lapland: 1732, *Linnaeus s.n.* (lectotype, designated by Edgar & Connor, in Edgar (1998: 556), LINN-85.7!; isotype, S!).

Avena tolucensis Kunth, Nov. Gen. Sp. 1: 148. 1816. *Trisetum tolucense* (Kunth) Kunth, Revis. Gram. 1: 101, t. 60. 1829. *Trisetum spicatum* subsp. *tolucense* (Kunth) Hultén, Svensk Bot. Tidskr. 53: 222. 1959. TYPE: Mexico: "crescit in apricis, frigidis, prope urbem mexicanam Toluca, alt. 1380 hexap.," *Humboldt & Bonpland s.n.* (holotype, P!; isotypes, BAA-3419 fragment ex K!, BAA-3420 fragment ex P!).

Trisetum nivosum E. Fourn., Mexic. Pl. 2: 107. 1886. *Trisetum spicatum* var. *nivosum* (E. Fourn.) Louis-Marie, Rhodora 30: 239. 1928 [1929]. TYPE: Mexico. Nevado de Toluca, Sep. 1865, *Hahn s.n.* (lectotype, designated by Finot (2003b: 688), P!; isotype, US-fragment ex P-Fourn!).

Perennial, caespitose; culms 9–50 cm tall, erect, densely pubescent below the inflorescence, the trichomes antrorse above, retrorse below; nodes 1 or 2. Leaf sheaths 1–3(–6) cm long, glabrous; ligule 0.5–1 mm long, minutely denticulate; blades 1–4 cm × 1–1.5 mm, flat, conduplicate toward the apex, glabrous to pubescent, sometimes scabrous or ciliate on the margins, the upper blade 1–5 cm long. Panicles 2.5–7(–10) × 0.5–1.3(–2) cm, spiciform, green to purple, shining, usually interrupted on the lower portions; rachis pubescent. Spikelets 4.5–5.5 mm long, (1)2-flowered; pedicels pubescent; rachilla ca. 1 mm long with trichomes 0.5–1 mm long; glumes subequal, wide, shorter than the spikelet, or the first glume somewhat shorter and narrower than the second glume, scabrous or more rarely ciliate on the keel; first glume 3.7–4.8 mm long, lanceolate to ovate-lanceolate, 1-nerved; second glume 4.5–5.5 mm long, ovate, 3-nerved; lemmas 3.8–5 mm long, glabrous, purplish toward the base, awned; margins hyaline; apex 2-aristate; awn 3.5–5 mm long, borne on the upper third or upper fourth, geniculate to curved, sometimes slightly twisted, scabrous, purplish; callus obtuse with trichomes 0.3 mm long; paleas 3–4 mm long, free from the lemma, shorter to slightly longer than the lemma, hyaline, 2-nerved, the keels scabrous; lodicules 0.6 mm long, hyaline, 2-lobed at the apex; ovary glabrous. Caryopses 2–2.8 mm long, ca. 0.6 mm wide; endosperm liquid.

Anatomy and micromorphology. Ligule apices have long cells and papillate cells with trichomes absent; epidermis with rectangular long cells with straight side walls, without trichomes, hooks, or stomata. Leaf blades in transverse section have prominent ribs with furrows deeper than one half the leaf thickness; adaxial and abaxial girders present; marginal sclerenchyma present; adaxial epidermis with inconspicuous bulliform cells; abaxial epidermis without trichomes and only few prickles present.

Distribution. Cosmopolitan and widespread. Hultén (1959) and Clebsch (1960) gave a detailed account of the distribution of *Trisetum spicatum*. In Mexico and Central America *T. spicatum* is usually found between 1900 and 4500 m.

Comments. *Trisetum spicatum* has been considered a complex, with many subspecies or varieties (Louis-Marie, 1928–1929; Hultén, 1959). Louis-Marie recognized 14 varieties and Hultén (1959) divided *T. spicatum* into 22 infraspecific taxa, including 14 subspecies and 8 varieties. In a phenetic study, Randall and Hilu (1986) concluded that the morphological variation is extreme and does not support the recognition of infraspecific taxa. In this treatment we interpret *T. spicatum* in a stricter sense, revalidating *T. rosei* and raising *T. spicatum* var. *barbatipaleum* to specific status. However, *T. spicatum* remains an extremely variable taxon with a large number of synonyms. In this revision we have included only those synonyms that occur in the study area, in addition to the basionym and its nomenclatural synonyms.

Specimens studied. DOMINICAN REPUBLIC. **Distrito Nacional:** Santo Domingo, Tierra de Ocoa, Prov. de Azua, San José de Ocoa, Cuchilla del Pino Atravesado, 1 Mar. 1929, *Ekman 11714* (S); Cordillera Central, Prov. de la Vega, Pico del Valle Nuevo, 15 Oct. 1929, *Ekman 13759* (S). **Barahona:** Cordillera de Baharuco, Tierra de Los Comisarios, 29 Aug. 1926, *Ekman 6803* (S). MEXICO. **Durango:** in montibus Convalli Mexicani prope aguae stagni seu fluitans, Aug. 1857, *Shaffner 57* (P). **Hidalgo:** Sierra de Pachuca, 21 July 1901, *Pringle 9603* (US). **México:** Nevado de Toluca, 5 Sep. 1958, *Hernández X 10197* (US); Nevado de Toluca, en el cráter, 25 Sep. 1892, *Pringle 4303* (S, US); Nevado de Toluca, cráter, Nov. 1907, *Diguet s.n.* (P); Mt. Popocatepetl, *Hitchcock 5996* (US); Valle de Mexico, falda de Ixtaccihuatl, 1 May 1952, *Matuda 26101* (US); Nevado de Toluca, 12 July 1938, *Balls 5025* (US); Volcán Toluca, 9 Sep. 1893, *Nelson 17* (US); Ixtaccihuatl, above timberline, Oct. 1905, *Purpus 1617* (US). **Jalisco:** Nevado de Colima, 26 Aug. 1958, *Beaman 2357* (US). **Puebla:** Mt. Orizaba, between timber and snow line, *Hitchcock 6258* (US); Mt. Orizaba, alpine region, Nov. 1906, *Rose 1270* (US).

10. Trisetum durangense Finot & P. M. Peterson, sp. nov. TYPE: Mexico. Durango: Sierra Madre Occidental, 56 km W of Durango on Hwy. 40, 2400 m, 29 Sep. 1988, *P. M. Peterson & C. R. Annable 6034* (holotype, US!). Figure 2.

Planta perennis; culmi glabri vel scabri sub panicula; vaginae pilosae, internodia paulo breviores vel aequales; ligula 3–6(–7) mm longa, acuta, lacerata; laminae conduplicatae, rigidae, 15–50 cm × 1–4 mm, subtus scabrae, supra scabrae vel sparse pilosae; paniculae 15–22 × 5–20 cm, laxae; rhachis scabra; spiculae 7–9 mm longae, 2(3)-florae; glumae subaequales, quam anthoecia contigua minores; gluma inferior quam superior brevior angustiorque, 5–6 mm longa; gluma superior 6–9 mm longa; spicula inferior 7–9 mm longa; lemmata pilosa, 5-nervia, 4-aristulata; callus pilosus; rhachilla pilosa, 2 mm longa; palea 5.8–7 mm longa; lodiculae 0.7–1.1 mm longae; stamina 3; ovarium ad apicem breve pilosum.

Perennial, caespitose, short rhizomatous; culms 75–110 cm tall, glabrous or retrorsely scabrous below the panicle; nodes 3, pubescent. Leaf sheaths 11–23 cm long, pilose, as long as or shorter than the internodes, with the membranous margin on one side sometimes projecting upward as long as a sheath-auricle; ligule 3–6(–7) mm long, acute, lacerated above; blades 15–50 cm × 1–4 mm, narrow, flat to conduplicate, rigid, strongly scabrous on the abaxial surface, scabrous and sparsely pubescent on the adaxial surface, ciliate on the margins. Panicles 15–22 × 5–20 cm, lax, drooping, open, pyramidal; branches appressed or ascending to spreading 0 to 75º from the culm axis, branches in 4 or 5 verticillate whorls per panicle, each whorl composed by 4 to 6 branches, apical branches 3–7 cm long, the lower branches 8–14 cm long; rachis, branches and pedicels strongly scabrous, capillary, bearing spikelets on the distal ends. Spikelets 7–9 mm long, 2(or 3)-flowered; glumes equal to subequal, similar in shape, as long as the spikelet or slightly shorter than the spikelet (first); first glume 5–6 mm long, lanceolate, slightly shorter and narrower than the second glume, 3-nerved, scabrous on the keel, apex acute; second glume 6–9 mm long, lanceolate, 3-nerved, apex acute; lemmas 7–8 mm long, awned near the middle, pilose especially below the awn insertion, 5-nerved, the nerves conspicuous toward the apex but vanishing toward the base of the lemma; margins of the lemma flat; apex 2-lobed, the lobes acute with the intermediate and marginal nerves prolonged into 4 short apical awns; awn 7–10 mm long, geniculate and twisted, golden brown, exserted; callus pubescent, the trichomes ca. 1 mm long; rachilla ca. 2 mm long, pubescent; paleas 5.8–7 mm long, hyaline, 2-nerved, the nerves ciliate; lodicules 0.7–1.1 mm long, ciliate at the apex; anthers 2–3 mm long, curved trichomes; ovary ca. 1 mm long, covered with short, curved and shining trichomes near the apex. Caryopses 2–2.7 × ca. 0.7 mm; endosperm soft.

Anatomy and micromorphology. Ligule apex composed of trichomes and some papillose cells; ligule epidermis composed of long cells with straight walls; prickles absent on the dorsal surface, only present at margins; macrohairs and stomata absent. Transversal section of the leaf blade with conspicuous adaxial ribs; vascular bundles with adaxial girders T-shaped; abaxial girders united forming a continuous band of abaxial sclerenchyma; abaxial epidermis with macrohairs and abundant prickles; epidermal long cells with undulate lateral walls; short cells present in costal and intercostal zones; stomata absent in abaxial epidermis.

Distribution. Known only from the state of Durango, *Trisetum durangense* occurs in open pine forests between 2400 and 2600 m.

Comments. Trisetum durangense is distinguished by its pilose sheaths; pubescent nodes; strongly scabrous blades; panicle with rachis, branches, and pedicels strongly scabrous; long, pilose lemmas; and an ovary with short, curved, and shining trichomes at the apex. The presence of these apical trichomes on the ovary is found in several taxa, including *T. cernuum* Trin. and *T. canescens* Buckley from North America, and *T. hirtiflorum* Hack., *T. caudulatum* Trin. var. *correae* Nicora, and *T. longiglume* Hack. var. *longiglume* from South America. *Trisetum durangense* is the only species in subgenus *Deschampsioidea* with pubescent lemmas and with an ovary with curved and

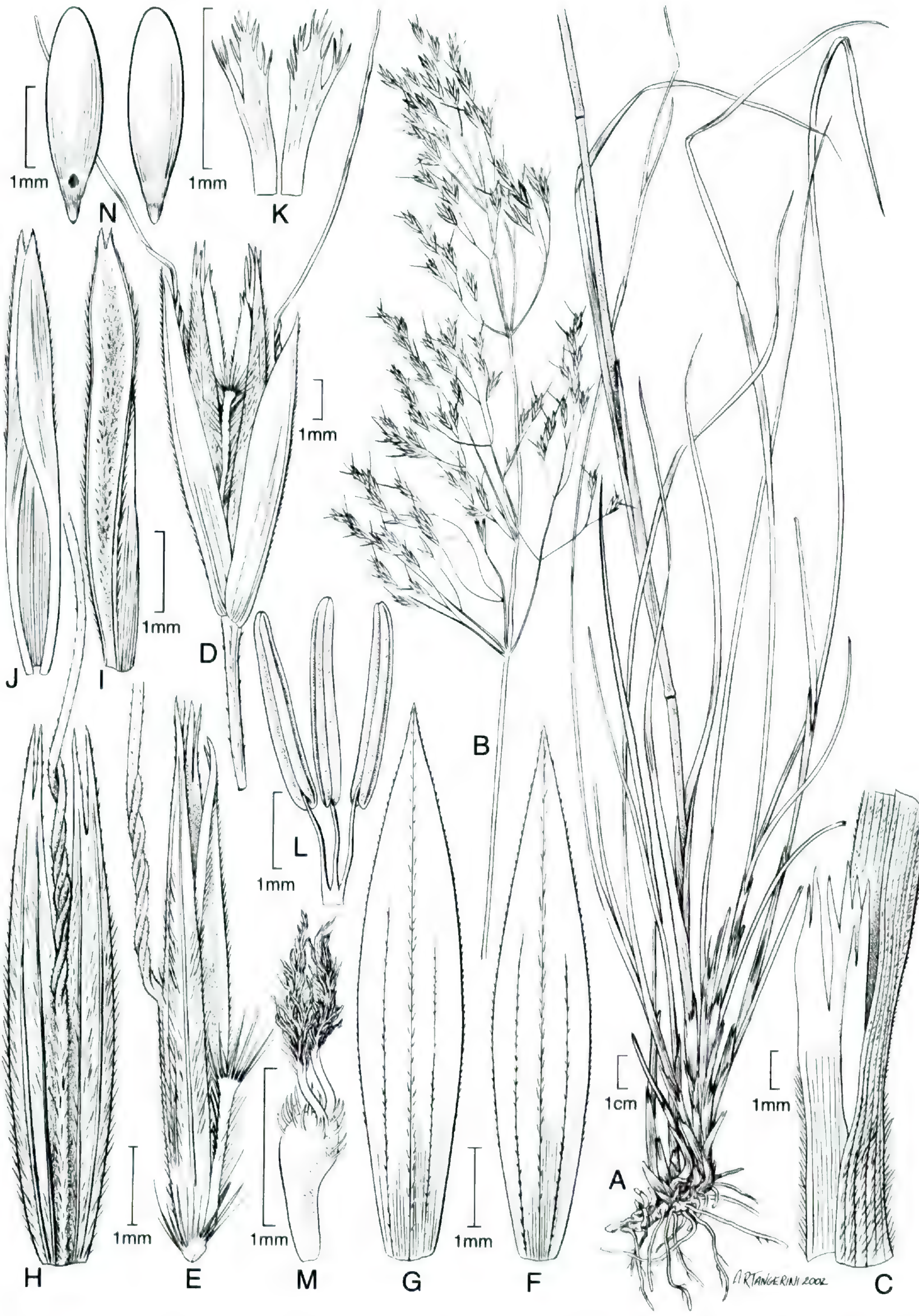

Figure 2. *Trisetum durangense* (*Peterson & Annable 6034*). —A. Habit. —B. Inflorescence. —C. Sheath, ligule, and portion of the blade. —D. Spikelet. —E. Floret. —F. First glume, dorsal view. —G. Second glume, dorsal view. —H. Lemma, dorsal view. —I. Palea, dorsal view. —J. Palea, ventral view. —K. Lodicules (2). —L. Stamens (3). —M. Pistil. —N. Caryopses (2).

shining trichomes near the apex. *Trisetum durangense* appears closely related to *T. viride* and can be easily distinguished from the latter by possessing pilose lemmas (glabrous in *T. viride*) and pubescent ovaries (glabrous in *T. viride*).

Paratypes. MEXICO. **Durango:** Mpio. de Durango, Parque El Tecuán, 58 km W of Durango, 20 Sep. 1984, *F. Casillas, R. Flores & F. Ruiz 9* (CIIDIR); 56 km W of Durango on Hwy. 40 toward Mazatlán, 23°54′45.7″N, 105°01′10.0″W, 6 Oct. 2002, *P. M. Peterson & L. E. Brothers 16964* (CONC, US); ca. 28 mi. N of Unidos Venceremos on road toward San Miguel de Cruces, 24°17′49.8″N, 105°29′32.2″W, 7 Oct. 2002, *P. M. Peterson & L. E. Brothers 16985* (CONC, US).

11. Trisetum martha-gonzaleziae P. M. Peterson & Finot, sp. nov. TYPE: Mexico. Durango: El Mezquital, 25 km de Los Charcos por camino a La Guajolota, 2110 m, 14 Mar. 1985, *M. González-Elizondo et al. 1645* (holotype, CIIDIR!). Figure 3.

Planta perennis; culmi glabri, striati, 3-nodi, 75–100 cm alti; vaginae glabrae, striatae, quam internodia breviores; ligula 0.5–1 mm, ovata; laminae planae vel convolutae, rigidae; panicula contracta, acuta, 10–20 × 1.5–2(–4) cm; spiculae biflorae (triflorae), 7.5–9 mm longa; glumae equales, 7.5–9 × 0.8–1.1 mm; lemmata glabra ad apicem bidentata; callus pilosus; ovarium pilosum.

Perennial; culms 75–100 cm tall, glabrous, striate, nodes 3, glabrous, dark. Leaf sheaths 3–10 cm long, glabrous, striate, shorter than the internodes, ciliate on the margins near the summit; ligule 0.5–1 mm long, longer in vegetative culms, ovate, slightly cleft at the apex, minutely denticulate-ciliate at the apex, glabrous on the dorsal surface; blades 10–30 cm × 2–3.5 mm, flat or convolute, stiff, scabrous on both sides. Panicles 10–20 × 1.5–2(–4) cm, contracted, subspiciform, acute, tinged with gold and purple, the branches semi-verticillate, each whorl composed of 5 or 6 branches, the lowest branch up to 5 cm long; rachis glabrous. Spikelets 7.5–9 mm long, 2(3)-flowered; pedicels glabrous; rachilla 1.4–1.5 mm long, densely pubescent, the trichomes ca. 1.5 mm long; glumes 7.5–9 mm long, 0.8–1.1 mm wide, equal, longer than the spikelet, weakly purple at the base, yellow at the apex, the keel slightly scabrous, the apex acute; lemmas ca. 5 mm long, glabrous, 5-nerved, rounded in cross section, bidentate at the apex, the intermediate nerves reaching the apex or prolonged beyond the apex as very short hyaline setae; awn ca. 5 mm long, inserted (1.5 mm from the base) near the middle or lower third, strongly twisted, geniculate, as long as the lemma; callus obtuse, pilose, the trichomes 1–1.2 mm long; palea ca. 5 mm long, about as long as or longer than the lemma, 2-nerved, the nerves well apart, tinged with purple and slightly scabrous; lodicules ca. 0.5 mm long, bilobed at the apex; ovary pilose.

Distribution. Endemic to Mexico (Chihuahua and Durango) between 2110 and 2450 m.

Paratypes. MEXICO. **Chihuahua:** 53 mi. W of Balleza and 5.5 mi. E of Guachochi, 19 Sep. 1991, *Peterson et al. 10784* (US). **Durango:** Mpio. El Mezquital, a 5 km del entronque del camino de Charcos a El Mezquital, 19 Mar. 1985, *O. García 82* (CIIDIR); Mpio. El Mezquital, alrededores de Santa María Ocotán, Nov. 1985, *M. González-Elizondo s.n.* (CIIDIR).

Etymology. This species honors the Mexican botanist Martha González-Elizondo, collector of the type specimen.

12. Trisetum palmeri Hitchc., Contr. U.S. Natl. Herb. 17: 325. 1913. TYPE: Mexico. Durango: Otinapa, 25 July–5 Aug. 1906, *E. O. Palmer 342* (holotype, US-571365!; isotypes, GH!, MO-3056877!).

Perennial, caespitose; culms 60–100 cm tall, glabrous. Leaf sheaths glabrous or scabrous; ligule 3–6 mm long, truncate, dentate, conspicuously ciliate at the apex, glabrous on the dorsal surface; leaf blades 10–20 cm × 1–3(–5) mm, involute or flat, stiff, scabrous, sometimes glaucous. Panicles 10–20 × 2–6 cm, lax, open, somewhat narrow, the branches 4 to 6, verticillate, the branches in distant whorls; rachis and pedicels glabrous. Spikelets 5–6.5 mm long, 2- or 3-flowered; rachilla ca. 2 mm long, pubescent, the trichomes 0.5–1(–1.4) mm long; glumes subequal, linear-lanceolate, both glumes shorter than the spikelet, the margin hyaline, the keel smooth or only slightly scabrous; apex acute; first glume 3.5–4.5 mm long, 1-nerved, slightly shorter and narrower than the second; second glume 4–5 mm long, 3-nerved; lemmas 4–5.3 mm long, somewhat fragile, translucent, terete, scabrous toward the apex, awned, the awn borne at the middle or upper third, 5-nerved, the nerves conspicuous below and vanishing toward the apex, or more rarely prolonged in 4 very short awns; apex 2-lobed, the lobes obtuse, sometimes erose; awn 5–7 mm long, geniculate and twisted, exserted; callus with trichomes, the trichomes 0.5–1 mm long or less; paleas 4–5.5 mm long, equal to slightly longer than the lemma, free; anthers 2–2.5 mm long; ovary glabrous. Caryopses not seen.

Anatomy and micromorphology. Ligule apices have short stiff trichomes and some papillate cells, epidermis with long cells rectangular to fusiform with straight side walls, hooks present; no tri-

Figure 3. *Trisetum martha-gonzaleziae* (*Gonzalez et al. 1645*). —A. Habit. —B. Sheath, ligule, and portion of the blade. —C. Spikelet. —D. Florets (2). —E. Floret. —F. Palea with rachilla, dorsal view. —G. Palea, lodicules, pistil, and stamens, ventral view. —H. Pistil.

chomes or stomata were observed. Leaf blades in transverse section are without a well-developed keel but have well-developed ribs; furrows more than half the leaf thickness, bulliform cells in assemblages of 4 to 9 in fan-shaped groups at the bottom of the furrows; trichomes present on the adaxial epidermis only; continuous abaxial sclerenchyma band present; first- and second-order vascular bundles with adaxial and abaxial girders, the adaxial ones T-shaped, marginal bundles only with adaxial girder; stomata present on adaxial epidermis only, marginal sclerenchyma present; epidermis showed costal/intercostal differentiation, hooks both in costal and intercostal zones, cork cells and silica bodies in pairs; no stomata or trichomes were seen.

Distribution. Endemic to Mexico (Chihuahua, Coahuila, Durango, Jalisco, Nuevo León, Sinaloa, and Sonora) between 2700 and 3400 m (Espejo-Serna et al., 2000; Finot, 2003b).

Comments. Hitchcock (1913) pointed out that *Trisetum palmeri* is closer to *Deschampsia* than to *Trisetum*; however, he described the species under *Trisetum* on the basis of the glumes shorter than the florets. *Trisetum palmeri* was synonymized with *T. viride* by Hernández-Torres and Koch (1988), from which it differs in having more rigid leaves and a longer ligule (3–6 mm long). *Trisetum viride* has a short ligule (0.5–1(–2) mm long).

Specimens studied. MEXICO. **Coahuila:** 55.3 km SE of Saltillo and 16.6 km SE of Jame on road to Sierra La Viga, 26 Sep. 1990, *Peterson et al. 10065* (US). **Durango:** Sierra Madre Occidental, 2 mi. N of Hwy. 40 on road to Neveros, 24 Oct. 1995, *Peterson et al. 13424* (US); 3.2 mi. S of La Peña on road toward La Puerta, 15 Sep. 2003, *Peterson et al. 17786* (CIIDIR, US); 14.6 mi. S of Tepehuana and 4.7 mi. N of Mesa La Gloria, 11 Sep. 2003, *Peterson & F. Sánchez-Alvarado 17743* (CIIDIR, US). **Nuevo León:** Sierra Madre Oriental, 11.4 mi. W of Dieciocho de Marzo up road toward Cerro Potosi, 18 Oct. 1995, *Peterson & Knowles 13336* (US).

13. Trisetum pinetorum Swallen, Phytologia 4(7): 424. 1953. TYPE: Guatemala. Quezaltenango: Volcán Santo Tomas, 22 Jan. 1940, *J. A. Steyermark 34824* (holotype, F-1048257 not seen; isotype, US-2236478 ex F!).

Perennial; culms 35–70 cm tall, glabrous. Leaf sheaths glabrous, with the margin extended up as a sheath-auricle 3 mm long, as long as or longer than the ligule; ligule 2–3 mm long, hyaline, truncate, the apex denticulate, glabrous on the dorsal surface; blades 1–2 mm wide, flat, glabrous. Panicles 8–15 × 0.6–1 cm, spiciform, narrow, densely flowered, interrupted, green; branches 1–3 cm long, closely appressed and ascending; rachis glabrous to slightly scabrous. Spikelets 6.5–7 mm long, 2-flowered; glumes subequal, ovate-lanceolate, acute at the apex, green, the margins hyaline, the keel slightly scabrous, both glumes slightly shorter than the spikelet; first glume 5–6 mm long, 1- to 3-nerved; second glume ca. 6 mm long, 3-nerved; lemmas ca. 6 mm long, scabrous near the apex, 5-nerved, awned from the middle or lower third, the margins hyaline and involute below, the apex hyaline and deeply bidentate, with 4 hyaline setae formed by the prolongation of the intermediate and marginal nerves beyond the apex; awn 10–12 mm long, geniculate and twisted; callus obtuse with trichomes ca. 1 mm long; paleas 3–4 mm long, shorter than the lemma and enclosed by the involute margins of the lemma; anthers ca. 1.5 mm long; ovary glabrous. Caryopses not seen.

Distribution. Guatemala and Mexico. Espejo-Serna et al. (2000) cited *Trisetum pinetorum* for Chiapas, Mexico.

Comments. The above description is based only on study of the type specimen at US and the original description. However, the Latin paragraph of the original description by Swallen (1953) mentioned 3-flowered spikelets, and the English paragraph mentioned 2-flowered spikelets. Spikelets with 3 florets were not found in the specimen examined. Though the subspiciform panicle of *T. pinetorum* resembles the species of *Trisetum* subg. *Trisetum* sect. *Trisetaera*, this species has a lemmatal apex with four setae, and the awn is borne on the middle of the lemma.

14. Trisetum spellenbergii Soreng, Finot & P. M. Peterson, sp. nov. TYPE: Mexico, Chihuahua: Mpio. Ocampo, Parque Nacional de Cascada Basaseachic, 2100 m, on nearly barren rock at overlook ca. 1 km S of Cascada, 3 Oct. 1986, *R. W. Spellenberg, R. J. Soreng, R. Corral & T. Lebgue 8654* (holotype, US!; isotypes, ESAHE!, ID!, K!, MEXU!, MO!, NMC!, RSA!, SI!, TAES!). Figure 4.

Planta rhizomatosa; culmi 40–60 cm alti, glabri; vaginae quam internodia longiores, inferiores pilosae, superiores glabrae; laminae 20–30 cm × 2–3.5 mm, planae, subtus glabrae, supra sparse pilosae; ligula 4.5–6 mm longa, glabra, lacerata; panicula 9–14 × 2–8 cm, laxa; spiculae 7–9 mm longae, (4)5–6-florae; glumae subaequales; gluma inferior 5.5–6.5 × 0.3–0.5 mm, quam superior paulo brevior, 1-nervia; gluma superior 6.5–7.5 × 0.6–0.8 mm; lemmata glabra, 5-nervia, apice hialino; arista 8–12 mm longa, dorso medio inserta; callus pilosus; palea 3.5–5 mm longa, quam lemma sua brevior; lodiculae ad apicem bilobulatae, ciliatae; stamina 3; ovarium glabrum.

Perennial, with short rhizomes; culms 40–60 cm

Figure 4. *Trisetum spellenbergii* (*Spellenberg, Soreng, Corral & Lebgue 8654*). —A. Habit. —B. Inflorescence. —C. Sheath, ligule, and portion of the blade. —D. Spikelet. —E. Floret. —F. First glume, dorsal view. —G. Second glume, dorsal view. —H. Lemma, dorsal view. —I. Palea, ventral view. —J. Palea, dorsal view. —K. Palea, lodicules, and pistil. —L. Lodicules (2). —M. Stamen. —N. Pistil.

tall, geniculate at the base, glabrous; nodes 2 to 4, glabrous. Leaf sheaths glabrous, longer than the internodes, the lower sheaths loose and pilose, the upper ones open only at the apex; margins membranous sometimes on one side projecting upward as a sheath-auricle as long as the ligule; ligule 4.5–6 mm long, scabrous on the dorsal surface; apex deeply lacerate, without cilia; blades 20–30 cm × 2–3.5 mm, flat, soft, glabrous on the lower surface, scabrous above, with or without a few long trichomes on the upper surface; uppermost culm leaf blade 10–20 cm long. Panicles 9–14 × 2–8 cm, lax, open, exserted; branches in 3 to 5 whorls of 2 to 5 branches per node, each branch bearing spikelets to near the base; lower branches 3.5–5 cm long. Spikelets 7–9 mm long, (4)5- or 6-flowered; rachilla ca. 1.5 mm long, pubescent, the trichomes 1–1.5 mm long, the rachilla prolonged beyond the uppermost floret bearing a reduced floret; glumes 5.5–7.5 mm long, shorter than the spikelet, green, purple to the apex and margin; keel smooth or slightly scabrous; first glume 5.5–6.5 mm long, slightly shorter than the second, 1-nerved; second glume 6.5–7.5 mm long; lemmas 4–6.5 mm long, glabrous, conspicuously 5-nerved, awned; intermediate nerves not extended as apical awns; marginal nerves vanish below the apex; apex bilobed, the lobes each ca. 2 mm long; awn 8–12 mm long, borne on the middle of the dorsal surface, twisted at the base, geniculate, usually twice as long as the lemma; callus pubescent, the trichomes ca. 1 mm long; paleas 3.5–5 mm long, shorter than the lemma, 2-nerved, the nerves scabro-ciliated; lodicules 1–1.5 mm long, the apex entire or with 2 short and unequal lobes, ciliate; anthers 1.2–2.5 mm long; ovary glabrous. Caryopses not seen.

Anatomy and micromorphology. Sheath ligule apex is composed of long cells with a few very short trichomes and the epidermis with prickles principally on the lower half and margins, no trichomes or stomata seen. Leaf blades in transverse section keeled, with prominent adaxial ribs, furrows between ribs more than one half the thickness; sclerenchyma of first- and second-order vascular bundles with adaxial and abaxial girders; adaxial girders T-shaped, abaxial girders I-shaped; marginal sclerenchyma present; epidermis with costal/intercostal zones differentiated, the intercostal zone only with long cells more or less rectangular with straight side walls, and costal zone with cork cells and silica bodies in short rows; adaxial epidermis with short trichomes, bulliform cells inconspicuous; abaxial epidermis with hooks, stomata present only on the adaxial surface.

Distribution. *Trisetum spellenbergii* is endemic to Chihuahua and Sonora, Mexico.

Comments. *Trisetum spellenbergii* is morphologically similar to *T. viride* but can be separated from the latter species by the presence of rhizomes (vs. absent in *T. viride*), its shorter stature (culms 40–60 cm tall in *T. spellenbergii* vs. culms 50–150 cm tall), soft and glabrous blades (vs. stiff and glaucous blades), spikelets with a greater number of florets (4- to 6-flowered in *T. spellenbergii* vs. 2- or 3-flowered), and lemmas with long bilobed apices (the lobes ca. 2 mm long in *T. spellenbergii* vs. less than 0.5 mm long and bidentate).

Etymology. The specific epithet honors Richard William Spellenberg (1940–) a Mexicophile and plant systematist at New Mexico State University.

Paratype. MEXICO. **Sonora:** Sierra Madre Occidental, 9.6 mi. E of Maycoba on Hwy. 16 toward Yepachic, 1420 m, 28°26′13″N, 108°33′05″W, 14 Oct. 1992, *P. M. Peterson & C. R. Annable 12509* (US).

15. Trisetum tonduzii Hitchc., N. Amer. Fl. 17(8): 558. 1939. TYPE: Costa Rica. Mount Poás, 2460 m, Nov. 1896, *A. Tonduz 10749* (holotype, US-358711!).

Perennial with rhizomes; culms 30–85 cm tall, erect, glabrous. Leaf sheaths glabrous, usually with trichomes at the apex, with one of the sides extended up as a sheath-auricle; ligule 1–3 mm long, truncate, dentate, ciliate; blades 3–21 cm × 2–6 mm, flat or involute, stiff, glabrous, occasionally loosely pubescent above. Panicles 6–15 × 2–10 cm, lax, open, ovoid-pyramidal, with ascending glabrous branches, usually as long as wide, purple; rachis glabrous; branches up to 8 cm long, densely flowered above, verticillate, up to 7 per node. Spikelets 4.5–6.5 mm long, 2-flowered; pedicels glabrous, scabrous distally; rachilla 1–2 mm long, pubescent, the trichomes 3 mm long; glumes 4–6.5 mm long, equal to subequal, nearly as long as the spikelet, usually purple, acute or awn-tipped, sometimes the first glume slightly shorter and narrower than the second glume; first glume 1- to 3-nerved; second glume 3-nerved; lemmas 3.8–6 mm long, lanceolate, glabrous, awned, slightly scabrous, 5-nerved, the nerves conspicuous toward the apex, the intermediate and marginal nerves prolonged beyond the apex as 4 setae or teeth, the setae 0.6–1 mm long; awn 7–13 mm long, borne a little above the middle, bent and twisted; callus pubescent, the trichomes 1.2–1.7 mm long; paleas 2.8–5.7 mm long, slightly shorter than the lemma, free from the lemma; lodicules truncate at the apex; anthers 1–2

mm long, purple; ovary glabrous. Caryopsis 2 mm long; endosperm soft.

Chromosome number. $n = 14$ (Pohl, 1980).

Anatomy. Leaf blades in transverse section are without well-developed keels or well-developed ribs, furrows more than one half the leaf thickness, bulliform cells in groups of 4 or 5 arranged in fan-shaped groups; trichomes absent in both epidermes; vascular bundles with adaxial and abaxial girders, except the marginal bundles; marginal sclerenchyma present; stomata present on the adaxial epidermis only; abaxial epidermis with intercostal rectangular long cells, costal short cells solitary or in cork cell-silica body pairs, prickles present intercostally.

Distribution. Costa Rica and Panama, 1500–3500 m.

Specimens studied. COSTA RICA. **Cartago:** 7 Aug. 1966, *Davidse & Pohl 842* (MO); Cantón de Oreamuno, P. N. Volcán Irazú, Cordillera Central, 09°58′49″N, 83°50′50″W, 28 Aug. 1995, *Morales & Dauphin 4801* (CR); Crater of Volcán Irazú, 7 Aug. 1966, *Pohl & Calderón 10230* (CR); Cratère du volcan Turrialba, 1 Jan. 1899, *Pittier 13082* (US); Sommet du Poas, Aug. 1890, *Pittier 841* (US); Potrero del alto, Volcán Poas, Nov. 1896, *Tonduz 214* (US); Sommet du Poas, Aug. 1890, *Pittier 2954* (P). **San José:** Las Nubes, 20–22 Mar. 1924, *Standley 38398* (US). PANAMA. **Chiriquí:** Chiriquí, 18 Mar. 1938, *White 54* (MO).

16. Trisetum viride (Kunth) Kunth, Revis. Gramin. 1: 101. 1829. Basionym: *Avena viridis* Kunth, Nov. Gen. Sp. 1: 147. 1816. *Trisetarium viride* (Kunth) Poir., Encycl. 5: 366. 1817. *Deyeuxia viridis* (Kunth) E. Fourn., Bull. Soc. Bot. France 24: 181. 1877. TYPE: Mexico. "Crescit in alta planitie Mexicana inter Salamanca et Queretaro, 900 hexap., *Humboldt & Bonpland s.n.* (holotype, P!; isotype, US-865584 fragment ex P!).

Trisetum altum Swallen, Phytologia 4: 423. 1953. TYPE: Guatemala. Sierra de las Minas, E of Finca Piamonte, El Progreso, 11 Feb. 1952, *J. A. Steyermark 43836* (holotype, US-1935005!; isotype, US-2208606!).

Deschampsia mexicana Swallen, Bol. Soc. Bot. Mexico 23: 28. 1958. *Trisetum mexicanum* (Swallen) S. D. Koch, Taxon 28: 233. 1979. TYPE: Mexico. Mexico: Valle de Bravo, 1800 m, 21 Nov. 1952, *E. Matuda 27795* (holotype, US-2119866!; isotype, MEXU not seen).

Perennial, caespitose; culms 50–150 cm tall; nodes 4, glabrous. Leaf sheaths shorter than the internodes, glabrous or pubescent, ciliate at the apex; ligule 0.5–1(–2) mm long, membranous; apex obtuse, minutely ciliate; blades 14–35 cm × 2–6(–9) mm, usually flat, somewhat stiff, sometimes convolute, glabrous with the adaxial face glaucous, the abaxial green. Panicles 12–30(–37) × 2–8 cm, lax, open or somewhat contracted, greenish to yellowish; lower branches 5–16 cm long, ascending, verticillate; rachis glabrous. Spikelets 5–8 mm long, 2- or 3-flowered; pedicels 1–3 mm long, glabrous; rachilla 1.5 mm long, pubescent, the trichomes 1.5–3 mm long especially near the apex, the lower portion subglabrous or pilose; glumes 3–7 mm long, subequal, somewhat translucent; first glume 3–6 mm long, 1-nerved, slightly shorter than the spikelet; second glume 4–7 mm long, 3-nerved, equaling or slightly longer than the spikelet; lemmas 4–7 mm long, glabrous, awned; apex bidentate, 5-nerved, the intermediate and marginal nerves sometimes prolonged as 2 or 4 hyaline setae ca. 0.2 mm long; awn 5–10 mm long, borne from the middle to the lower third or fourth, geniculate and twisted; callus obtuse, pubescent, the trichomes 0.5–1 mm long; paleas 3–6 mm long, shorter than the lemma, hyaline, 2-nerved, the keels scabrous; anthers 1–3.3 mm long; ovary glabrous. Caryopses 2–2.5 mm long; endosperm liquid.

Chromosome number. $2n = 28$ (Herrera-Arrieta, 2001).

Anatomy and micromorphology. Ligule apices have papillate cells and short trichomes; epidermal long cells elongated perpendicular to the vertical axis of the ligule, rectangular, with undulate side walls; no trichomes, prickles, or stomata were seen in the epidermis. Leaf blades in transverse section are without a well-developed keel but have well-developed ribs, furrows more than one half the leaf thickness, trichomes present only in the adaxial epidermis; first- and second-order vascular bundles with both adaxial and abaxial girders, the marginal bundles with sclerenchyma in small abaxial strands; abaxial epidermis with intercostal rectangular long cells with undulate side walls, costal short cells present as cork cell-silica body pairs, sometimes solitary; stomata and trichomes not seen, prickles present.

Distribution. Trisetum viride grows in Mexico and Guatemala between 1500 and 3100 m. In Mexico it occurs in the following states: Chihuahua, Chiapas, Durango, Guerrero, Guanajuato, Jalisco, México, Michoacán, Oaxaca, and Querétaro (Hernández-Torres & Koch, 1988; Espejo-Serna et al., 2000; Herrera-Arrieta, 2001).

Comments. Hernández-Torres and Engleman (1995) more recently performed an anatomical survey of *Trisetum* in Mexico and they considered *T. mexicanum* a distinct species. They noted that *T. mexicanum* could be distinguished by the size of

the bulliform cells, but no further morphological characteristics were discussed. We choose to place *T. mexicanum* as a synonym of *T. viride*.

Specimens studied. MEXICO. **Coahuila:** Sierra Madre Oriental, ca. 5 km E of Saltillo (Las Palapas) up camino de Quatro, 20 Sep. 2003, *Peterson et al. 17863* (CIIDIR, US). **Durango:** along Mazatlán–Durango hwy., 3–15 km toward El Salto from the Sinaloa boundary at El Palmito, 13 Apr. 1965, *McVaugh 23605* (US); 10 km N carretera Durango–Mazatlán, 6 Oct. 1978, *Koch & Sánchez 78155* (US); San Ramón, 21 Apr.–18 May 1906, *Palmer 128* (US); Sierra Madre Occidental, 2.4 mi. N of Borbollones, N of hwy. 40, 25 Oct. 1995, *Peterson et al. 13432* (US); 2 mi. N of Tepehuana on road toward Mezquital, 11 Sep. 2003, *Peterson & F. Sánchez-Alvarado 17739* (CIIDIR, US). **Guerrero:** entre Ayusinapa y Petatlán, 14 Dec. 1894, *Nelson 2123* (US); Teotepec, 11 May 1939, *Hinton et al. 14795* (US). **Oaxaca:** Sierra de San Felipe, 18 Sep. 1894, *Pringle 4919* (P, US).

17. Trisetum virletii E. Fourn., Mexic. Pl. 2: 108. 1886. TYPE: Mexico. San Luis Potosí: 1851, *Virlet 1304* (lectotype, designated by Finot (2003b: 675), P!; isotype, US-91219 fragment ex P-Fourn. 247!).

Trisetum bambusiforme E. Fourn., Mexic. Pl. 2: 108. 1886. TYPE: Mexico. In sylva de la desierta Vieja vallis Mexicensis, 3 Nov. 1865, *E. Bourgeau 1304* (holotype, P!; isotypes, GH not seen, US-fragment ex P-Fourn-248!; US-fragment ex MPU-Fourn-248!).

Perennial with rhizomes; culms 1.5–3 m tall, 5–7(–10) mm diam. below with extravaginal branches on the upper nodes, glabrous, bambusiform. Leaf sheaths minutely scabrous, longer than the internodes; ligule (2–)5–10 mm long, membranous, apex obtuse to truncate, laciniate and ciliate, the cilia up to 2 mm long; blades 30–45 cm × 5–13 mm, flat, minutely scabrous. Panicles 20–45 × 5–12(–20) cm, lax, ± open, pyramidal, dense, green or yellow-green; branches usually 10–15 cm long, verticillate; rachis glabrous. Spikelets 5–7.5 mm long, (3)4- or 5-flowered; pedicels 1–4 mm long, scabrous; rachilla 0.5–0.7 mm long, densely pubescent, the trichomes 2–3.3 mm long, more numerous at the apex; glumes unequal, acute to shortly awned, the first slightly shorter and narrower than the second, both glumes shorter than the spikelet, scabrous along the nerves; first glume (3–)4–5.1(–6) mm long, linear-lanceolate to lanceolate, 1-nerved; second glume 4–6(–8) mm long, lanceolate to ovate-lanceolate, 3-nerved; lemmas 4–6 mm long, scabrous, 5-nerved, awned, the nerves not conspicuous near the apex, somewhat rounded in cross section, the margins hyaline toward the apex; apex 2- or 4-dentate (sometimes appearing almost entire), the teeth short not prolonged as setae or awns; callus obtuse with a few short trichomes, the trichomes 0.5–1 mm long; awn 1.5–4(–4.5) mm long, borne on the upper third, geniculate, slightly twisted; paleas 3.5–5 mm long, shorter than the lemma, 2-nerved, the nerves scabrous; anthers 1.8–2.5(–3) mm long. Caryopses 1.5–2.5 mm long; endosperm liquid.

Chromosome number. $2n = 28$ (Tateoka, 1962).

Anatomy and micromorphology. Ligule apex has long cilia and short hair; epidermis composed of long cells with undulate side walls, with abundant prickles; no trichomes or stomata were seen. Leaf blades in transverse section are without a well-developed keel or ribs, furrows less than one half the leaf thickness with trichomes present on the adaxial epidermis only; vascular bundles with adaxial and abaxial girders; marginal sclerenchyma as a small rounded strand, stomata present in the adaxial epidermis only; bulliform epidermis present; adaxial epidermis with rectangular long cells with straight side walls, short costal cells present, stomata absent, prickles present.

Distribution. Endemic to Mexico (Chiapas, Distrito Federal, Durango, Guanajuato, Jalisco, México, Michoacán, Morelos, Puebla, Querétaro, San Luis Potosí, and Veracruz (Espejo-Serna et al., 2000; Herrera-Arrieta, 2001; Finot, 2003b). *Trisetum virletii* grows in moist woods between 2000 and 3500 m.

Specimens studied. MEXICO. **Distrito Federal:** Cerro Gordo, Cerro Cautillo Grande, ¼ km S of La Cima Station, just N and W of old hwy. 95, 12 July 1960, *H. Iltis, Koeppen & F. Iltis 152* (US). **Hidalgo:** along Hwy. 105 between Pachuca and Tampico, vicinity of Mineral del Monte, 20°08′N, 98°3′W, 27 Feb. 1987, *Croat & Hannon 65794* (SI ex MO). **Jalisco:** NNE-facing slopes of Volcán Colima, 19°38′N, 103°35′W, 31 Dec. 1978, *Iltis, Guzmán & Nee 1065* (US); SE slopes of Nevado de Colima, 2 Apr. 1951, *McVaugh 11721* (US); N slopes of Nevado de Colima, 2 Apr. 1949, *McVaugh 10161* (US). **México:** Mpio. Amecameca, cañada del cerro Venacho, 12 km al E de Amecameca, 23 Dec. 1976, *Koch 76337* (US); vicinity of La Cima railroad station, on top of the Serjana de Ajusco, 19°07′N, 99°12′W, 23 Jan. 1963, *Iltis & Iltis 1671-a* (US); Valle de Mexico, C. de León, 7 Jan. 1951, *Matuda 20892* (US); Amecameca, Cerro Venacho, 15 Feb. 1953, *Matuda et al. 28076* (US); Sierra de Las Cruces, 20 Apr. 1898, *Pringle 7571* (US); Ixtaccihuatl, Jan. 1906, *Purpus 1612* (US); Temascaltepec, Mesón Viejo, 12 Jan. 1932, *Hinton 2745* (US); Texcoco, ca. Cerro Texaltepec, 3 km SSE de San Pablo Ixayoc y 13 km SE Texcoco, 9 Nov. 1975, *Koch 75706* (US). **Michoacán:** vicinity of Morelia, 9 Feb. 1911, *Arsène 5410* (US); cool slopes of mountains near Patzcuaro, 21 Dec. 1891, *Pringle 3970* (US); Coalcomán, Barroloso, 3 Mar. 1941, *Hinton 15747* (US); Mt. Tancitaro, 22 July 1941, *Leavenworth & Leavenworth 1122* (US). **Morelos:** Tres Marías, 16 Dec. 1907, *Pringle 15002* (US); 5 mi. S of Morelos-Federal District border, 14 Mar. 1961, *King 4155* (US).

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APPENDIX 1. Subgeneric treatment of *Trisetum* in Mexico and Central America

Trisetum

Species, incertae sedis: *T. angustum, T. filifolium, T. pringlei*

Trisetum subg. **Trisetum**

Panicles spiciform or more rarely contracted to open. Spikelets usually 2- or 3-flowered; glumes lanceolate, unequal, glabrous or rarely pilose, shorter or longer than the spikelet; first glume 1(3)-nerved, usually shorter and narrower than the second; second glume 3(5)-nerved; lemmas lanceolate, glabrous or pilose, slightly keeled, laterally compressed, 5-nerved, the nerves prolonged beyond the 2-dentate apex as 2 or 4 setae, awned from the upper third; awn exserted, geniculate or merely divaricate, sometimes twisted; ovary glabrous or with short and shining trichomes at the apex. Caryopses compressed, soft, glabrous or with short trichomes at the apex; endosperm liquid or more rarely solid.

Trisetum subg. **Trisetum** sect. **Trisetum**

Species: *T. curvisetum, T. irazuense*

Trisetum subg. **Trisetum** sect. **Trisetaera** Asch. & Graebn., Syn. Mitteleur. Fl. 2: 270. 1895. TYPE: *Trisetum spicatum* (L.) K. Richt., Pl. Eur. 1: 59. 1890.

Panicle spiciform, narrow, densely flowered; rachis densely pilose to pubescent below the inflorescence. Spikelets 2- to 4-flowered, rarely 1- or (2)-flowered; glumes unequal, mostly shorter than the spikelet, sometimes longer.

Species: *T. barbatipaleum, T. ligulatum, T. rosei, T. spicatum*

Trisetum subg. **Deschampsioidea** (Louis-Marie) Finot, stat. nov. Basionym: *Trisetum* subsect. *Deschampsioidea* Louis-Marie, Rhodora 30(59): 211. 1928. TYPE: *Trisetum palmeri* Hitchc., lectotype, designated here.

Panicles lax, open, rarely spiciform. Spikelets 2- to 6-flowered; glumes 2, ± equal, lanceolate, keeled, muticous, glabrous, slightly shorter than or equaling the spikelet; first glume 1-nerved; second glume 3-nerved; lemmas lanceolate, membranous, with the apex and margins hyaline, glabrous or rarely hirsute, slightly rounded in cross section, 5-nerved, the nerves disappearing toward the apex or rarely prolonged beyond the 2-dentate apex in (2) or 4 setae, usually awned from the middle; awn geniculate; ovary usually glabrous or rarely with short trichomes at the apex. Caryopses compressed, soft, usually glabrous, rarely with short and shining trichomes at the apex.

Species: *T. durangense, T. martha-gonzaleziae, T. palmeri, T. pinetorum, T. spellenbergii, T. tonduzii, T. viride, T. virletii*

Comments. A lectotype was chosen because Louis-Marie (1928) cited two species without designating a type.

APPENDIX 2. List of names and synonyms. **Accepted names** are presented in bold and synonyms are *italicized.*

Acrospelion Besser ex Schult. & Schult. f. = **Trisetum**
Agrostis obtusata (Michx.) Steud. = **S. obtusata**
Aira koelerioides Peyr. = **P. koelerioides**
Aira mexicana Trin. ex E. Fourn. = **S. obtusata**
Aira obtusata Michx. = **S. obtusata**
Aira spicata L. = **T. spicatum**
Aira subspicata L. = **T. spicatum**
Aira truncata Muhl. = **S. obtusata**
Airopsis obtusata (Michx.) Desv. = **S. obtusata**
Avena airoides Koeler = **T. spicatum**
Avena deyeuxioides Kunth = **P. deyeuxioides**
Avena elongata Kunth = **S. interrupta** subsp. **interrupta**
Avena tolucensis Kunth = **T. spicatum**
Avena trichopodia J. Presl = **P. deyeuxioides**
Avena viridis Kunth = **T. viride**
Calamagrostis irazuensis Kuntze = **T. irazuense**
Calamagrostis longirostris Buckley = **S. interrupta** subsp. **interrupta**
Deschampsia koelerioides (Peyr.) Benth. = **P. koelerioides**
Deschampsia mexicana Swallen = **T. viride**
Deschampsia pringlei Scribn. = **P. pringlei**
Deyeuxia evoluta E. Fourn. = **P. deyeuxioides**
Deyeuxia gracilis E. Fourn. = **P. humilis**
Deyeuxia triflora Nees = **P. deyeuxioides**
Deyeuxia viridis (Kunth) E. Fourn. = **T. viride**
Eatonia annua Suksd. = **S. obtusata**
Eatonia densiflora E. Fourn. = **S. obtusata**
Eatonia obtusata (Michx.) A. Gray = **S. obtusata**
Eatonia obtusata var. *purpurascens* Vasey ex Rydb. & Shear = **S. obtusata**
Eatonia obtusata var. *robusta* Vasey ex L. H. Dewey = **S. obtusata**
Eatonia obtusata var. *robusta* Vasey ex Rydb. = **S. obtusata**
Eatonia pubescens Scribn. & Merr. = **S. obtusata**
Eatonia robusta (Vasey ex L. H. Dewey) Rydb. = **S. obtusata**
Graphephorum altijugum E. Fourn. = **P. koelerioides**
Graphephorum pringlei Scribn. ex Beal = **T. pringlei**
Koeleria obtusata Trin. ex Steud. = **S. obtusata**
Koeleria paniculata Nutt. = **S. obtusata**
Koeleria spicata Rchb. ex Willk. & Lange = **T. spicatum**
Koeleria subspicata (L.) Rchb. = **T. spicatum**
Koeleria truncata (Muhl.) Torr. = **S. obtusata**
Peyritschia E. Fourn.
Peyritschia deyeuxioides (Kunth) Finot
Peyritschia humilis (Louis-Marie) Finot
Peyritschia koelerioides (Peyr.) E. Fourn.
Peyritschia pringlei (Scribn.) S. D. Koch
Poa obtusata (Michx.) Link = **S. obtusata**
Rebentischia Opiz = **Trisetum**
Reboulea gracilis Kunth = **S. obtusata**
Reboulea obtusata (Michx.) A. Gray = **S. obtusata**
Reboulea obtusata var. *pubescens* (Scribn. & Merr.) Farw. = **S. obtusata**
Rupestrina Prov. = **Trisetum**
Rupestrina pubescens Prov. = **T. spicatum**
Sphenopholis Scribn.
Sphenopholis annua (Suksd.) A. Heller = **S. obtusata**
Sphenopholis hallii (Scribn.) Scribn. = **S. interrupta** subsp. **interrupta**
Sphenopholis interrupta (Buckley) Scribn.
Sphenopholis interrupta (Buckley) Scribn. subsp. **interrupta**
Sphenopholis interrupta subsp. **californica** (Vasey) Scribn.
Sphenopholis obtusata (Michx.) Scribn.

Sphenopholis obtusata fo. *purpurascens* (Vasey ex Rydb. & Shear) Waterf. = **S. obtusata**
Sphenopholis obtusata subsp. *lobata* (Trin.) Scribn. = **S. obtusata**
Sphenopholis obtusata subsp. *pubescens* (Scribn. & Merr.) Scribn. = **S. obtusata**
Sphenopholis obtusata var. *lobata* (Trin.) Scribn. ex B. L. Rob. = **S. obtusata**
Sphenopholis obtusata var. *pubescens* (Scribn. & Merr.) Scribn. ex B. L. Rob. = **S. obtusata**
Sphenopholis pubescens (Scribn. & Merr.) A. Heller = **S. obtusata**
Sphenopholis robusta (Vasey ex L. H. Dewey) A. Heller = **S. obtusata**
Trisetaria airoides (Koeler) Baumg. = **T. spicatum**
Trisetaria deyeuxioides (Kunth) Poir. = **P. deyeuxioides**
Trisetaria spicata (L.) Paunero = **T. spicatum**
Trisetarium Poir. = **Trisetum**
Trisetarium elongatum (Kunth) Poir. = **S. interrupta** subsp. **interrupta**
Trisetarium viride (Kunth) Poir. = **T. viride**
Trisetum Pers.
Trisetum subg. **Deschampsioidea** (Louis-Marie) Finot
Trisetum sect. **Trisetaera** Asch. & Graebn.
Trisetum sect. **Trisetum**
Trisetum subg. **Trisetum**
Trisetum subsect. *Deschampsioidea* Louis-Marie = **Trisetum** subg. **Deschampsioidea**
Trisetum airoides (Koeler) P. Beauv. ex Roem. & Schult. = **T. spicatum**
Trisetum altijugum (E. Fourn.) Scribn. = **P. koelerioides**
Trisetum altum Swallen = **T. viride**
Trisetum angustum Swallen
Trisetum bambusiforme E. Fourn. = **T. virletii**
Trisetum barbatipaleum (Hultén ex Veldkamp) Finot
Trisetum californicum Vasey = **S. interrupta** subsp. **californica**
Trisetum curvisetum Morden & Valdés-Reyna
Trisetum deyeuxioides (Kunth) Kunth = **P. deyeuxioides**
Trisetum deyeuxioides var. *pubescens* Scribn. ex Beal = **P. deyeuxioides**
Trisetum durangense Finot & P. M. Peterson
Trisetum elongatum (Kunth) Kunth = **S. interrupta** subsp. **interrupta**
Trisetum evolutum (E. Fourn.) Hitchc. = **P. deyeuxioides**
Trisetum filifolium Scribn. ex Beal
Trisetum filifolium Scribn. ex Beal var. **filifolium**
Trisetum filifolium var. **aristatum** Scribn. ex Beal
Trisetum fournieranum Hitchc. = **T. irazuense**
Trisetum gracile E. Fourn. = **T. irazuense**
Trisetum hallii Scribn. = **S. interrupta** subsp. **interrupta**
Trisetum humile Louis-Marie = **P. humilis**
Trisetum interruptum Buckley = **S. interrupta** subsp. **interrupta**
Trisetum interruptum E. Fourn. = **T. spicatum**
Trisetum interruptum UNRANKED *hallii* (Scribn.) Hitchc. = **S. interrupta** subsp. **interrupta**
Trisetum interruptum var. *californicum* (Vasey) Louis-Marie = **S. interrupta** subsp. **californica**
Trisetum irazuense (Kuntze) Hitchc.
Trisetum kochianum Hern. Torres = **P. pringlei**
Trisetum ligulatum Finot & Zuloaga
Trisetum lobatum Trin. = **S. obtusata**
Trisetum martha-gonzaleziae P. M. Peterson & Finot
Trisetum mexicanum (Swallen) S. D. Koch = **T. viride**
Trisetum nivosum E. Fourn. = **T. spicatum**
Trisetum palmeri Hitchc.
Trisetum paniculatum E. Fourn. = **T. viride**
Trisetum pinetorum Swallen
Trisetum pringlei (Scribn. ex Beal) Hitchc.
Trisetum rosei Scribn. & Merr.
Trisetum rosei var. *tenerum* Scribn. & Merr. = **T. rosei**
Trisetum rosei fo. *tenerum* (Scribn. & Merr.) Louis-Marie = **T. rosei**
Trisetum scabriflorum Hitchc. = **T. irazuense**
Trisetum scabrivalve Sodiro = **T. irazuense**
Trisetum spellenbergii Soreng, Finot & P. M. Peterson
Trisetum spicatum (L.) K. Richt.
Trisetum spicatum subsp. *tolucense* var. *barbatipaleum* Hultén = **T. barbatipaleum**
Trisetum spicatum subsp. *tolucense* (Kunth) Hultén = **T. spicatum**
Trisetum spicatum var. *barbatipaleum* Hultén = **T. barbatipaleum**
Trisetum spicatum var. *barbatipaleum* Hultén ex Veldkamp = **T. barbatipaleum**
Trisetum spicatum var. *nivosum* (E. Fourn.) Louis-Marie = **T. spicatum**
Trisetum subspicatum (L.) P. Beauv. = **T. spicatum**
Trisetum tolucense (Kunth) Kunth = **T. spicatum**
Trisetum tonduzii Hitchc.
Trisetum viride (Kunth) Kunth
Trisetum virletii E. Fourn.

REVISION OF *METASTELMA* (APOCYNACEAE–ASCLEPIADOIDEAE) IN SOUTHWESTERN NORTH AMERICA AND CENTRAL AMERICA[1]

Sigrid Liede[2] *and Ulrich Meve*[2]

Abstract

The revision of *Metastelma* (Apocynaceae–Asclepiadoideae) in southwestern North America and Central America (excluding the Caribbean) is based on field observations and study of herbarium specimens. Sixteen species are recognized (two of these split into two subspecific units, two into three subspecific units). Two new taxa, *M. barbigerum* var. *veracruzense* and *M. schlechtendalii* var. *arenicola*, are described. Two former species are reduced to subspecific rank (*M. arizonicum* subsp. *chiapense* and *M. californicum* subsp. *lanceolatum*) and two to varietal rank (*M. barbigerum* var. *liesneriana* and *M. schlechtendalii* var. *trichophyllum*). One taxon (*M. turneri*) is raised from varietal to species rank. Four new synonyms are recognized: *Ditassa mexicana* as synonym to *M. californicum* subsp. *lanceolatum*, *M. infimicola* as synonym to *M. eliasianum*, *M. macropodum* as synonym to *M. palmeri*, and *M. multiflorum* as synonym to *M. schaffneri*. The morphology of the North and Central American species of *Metastelma*, as well as habitats, distribution, and phenology, are described. In addition to the taxonomic descriptions, illustrations and distribution maps are presented for each species.

Key words: Apocynaceae, Asclepiadoideae, Central America, *Metastelma*, North America.

Metastelma R. Br. is an entirely American genus of Apocynaceae–Asclepiadoideae, with a distribution ranging from northern Argentina as far north as Texas. Its center of diversity lies in the Caribbean (these taxa are not considered herein). No reliable estimates on the number of species are available, because the concept of the genus has been subject to unusually large changes (see below). The number of published names stands at ca. 190—the number of species is probably around 70, with 16 found in southwestern North America and Central America (as detailed here), ca. 30 in the Caribbean (including eastern North America), and 20–25 in South America (Liede, unpublished observations).

Within the Asclepiadoideae, *Metastelma* belongs to the Asclepiadeae, the only tribe of Asclepiadoideae possessing pendent pollinia (Liede & Albers, 1994). The subtribal delimitation of the large tribe Asclepiadeae (ca. 100 genera, Liede & Albers, 1994) has been subject to much debate. In the first subtribal classification for the tribe, which was based solely on corona characters, Schumann (1895) placed *Metastelma* with its gynostegial, but purely staminal corona in the Asclepiadinae. He distinguished *Irmischia* Schltdl. because of its seemingly corolline corona and placed it in the Glossonematinae. Liede (1997), in an attempt to define more naturally delimited subtribes, placed *Metastelma* (including *Irmischia*) in the Metastelmatinae, after Kunze's (1997) study of floral morphology had supported its exclusion from Asclepiadinae. The Metastelmatinae sensu Liede (1997) constituted a large subtribe with members in both hemispheres. Recent molecular work (Liede & Täuber, 2000, 2002; Rapini et al., 2003; Liede et al., in prep.) has shown that the New World members of the Metastelmatinae sensu Liede (1997) form a clade of their own, the Metastelmatinae s. str., in close relationship to the two other subtribes restricted to the New World, Oxypetalinae and Gonolobinae (Liede, 1997; Rapini et al., 2003). *Orthosia*, often confused with *Metastelma*, forms a subtribe of its own together with *Jobinia* E. Fourn. and some former "*Cynanchum*" species (Liede et al., in prep.). Within the Metastelmatinae s. str., genus and species delimitation is still difficult, mainly

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due to the extremely diverse, but poorly known South American species. In South America, the species attribution between the florally very similar genera *Metastelma* and *Ditassa* is purely formal, placing species with a simple staminal corona in *Metastelma*, those with a double staminal corona in *Ditassa*. It is yet unknown whether reduction of the inner corona lobe has given rise to "*Metastelma*" species that need to be included in *Ditassa*, and it is also unknown whether *Ditassa*-type flowers have arisen independently more than once from *Metastelma*-type flowers by doubling of corona lobes. In South America, Rapini (2001) recently suggested transferring two *Metastelma* species (*M. hemipogonioides* Malme and *M. hatschbachii* Fontella & Marquete) to *Hemipogon* E. Fourn., a genus previously defined by a characteristic erect, slender habit with pendulous flowers, and the absence of a corona (Fournier, 1885). The two species combine the typical habit of *Hemipogon* with the corona structure of *Metastelma*, suggesting a close relationship between the two genera.

In Central America (and the Caribbean) in contrast, delimitation of *Metastelma* is by far less complex, even though the unfortunate inclusion of almost every small American asclepiad with twining habit and pendulous pollinia in *Cynanchum* by Woodson (1941) has led to considerable confusion. Prior to this (Schlechter, 1899), members of *Orthosia* Kunth have been confused with *Metastelma* even though they are clearly separable by a combination of a much more regular branching pattern, adaxially glabrous corolla lobes, and an annular corona.

Metastelma has never been revised over a larger geographical scale. This revision deals with all of mainland Central America, extending north to the southwestern United States, the northern distributional limit of the genus, and south to the Panama Canal, including the former Canal Zone. It is based on field observations in the U.S.A., Mexico, and Guatemala, and on study of more than 400 herbarium collections from the U.S.A., Mexico, and Central America. Previous records of *Metastelma* are dispersed in various floral treatments of different geographical scope and, in part, of considerable age (see below). Nevertheless, these records give a good reflection of species diversity throughout Central America. The highest diversity is found in the Sonoran desert, where Fishbein (1998) listed seven species for the Río Mayo area alone. To the north, diversity declines rapidly. Sundell (1994) listed two species for Arizona, and Shinners (1964) listed two for Texas. To the south, diversity declines as well. Wiggins (1980) listed two species for Baja California. Amazingly, two species are also listed for the small island of Socorro (Levin & Moran, 1989) (all hidden under "*Cynanchum*"), suggesting a considerable capacity for long-distance dispersal. For Mexico as a whole, Standley (1924) listed 14 species. Further south, species diversity remains low with five species listed for Guatemala, one each for Belize (Standley & Record, 1936) and Honduras (Standley, 1938a), two for El Salvador (Standley, 1925) (all hidden under "*Cynanchum*"). Two records are listed for Costa Rica (Standley, 1938b), but one of them, *M. filisepalum*, was only attributed to *Metastelma* with a question mark and is now excluded from the genus (see excluded species). For Nicaragua, Stevens (2001) listed three taxa, *M. trichophyllum* (*M. schlechtendalii* var. *trichophyllum*) and two unidentified species. Species A is identified here as *M. schlechtendalii* var. *schlechtendalii*, in which the attachment of the corona along the stipe is quite variable, and species B is identified as *M. pedunculare*. For Panama only one species is reported (D'Arcy, 1987), again under "*Cynanchum*."

The genus is taxonomically difficult not only because of its minute flowers, but also because 5 of the 15 species recognized here form widespread and variable complexes, the most extensive being *M. barbigerum* and *M. schlechtendalii*. This fact is reflected by the large number of subspecific units: subspecies for geographically well-separated taxa distinguishable by at least one distinct morphological character, and varieties for geographically less clear-cut taxa, distinguishable on the basis of a weaker morphological character, such as the indumentum. Like the other large American Metastelmatinae genera, *Metastelma* is a comparatively young genus still in the process of speciation and radiation (Liede et al., in prep.).

Apart from these widespread complexes, several species are more or less narrow endemics, most of these occurring in northern Mexico. However, the degree of endemism in *Metastelma* has been overestimated, because several species described as narrow endemics (e.g., *M. macropoda*, *M. sepicola*) were found to be indistinguishable from species described from another area during the present study. One species, *M. infimicola* from Panama, is identical to *M. eliasianum* described from Colombia, underlining the close relationship of the Panamanian flora with the Colombian one.

Finally, a handful of specimens exist that are either found far off the distribution area of the most closely related species or deviate considerably from the most closely related species. These specimens are discussed in the text under the most closely related taxon, but until more material becomes available, it seems premature to describe new spe-

cies based on what is probably an aberrant specimen. The material studied points to a considerable potential for long-distance dispersal, hybridization, and introgression, possibly resulting occasionally in atypical plants or typical plants in unexpected places.

It is difficult to propose a hypothesis about the relationships of the species studied, so only a few obvious relationships will be mentioned. *Metastelma barbigerum*, *M. schaffneri*, and *M. schlechtendalii* form a complex in which some specimens show considerable reticulation of characters. *Metastelma minutiflorum* and *M. latifolium* probably are vicariant species with coastal and inland preferences, respectively. *Metastelma mexicanum* shows some affinities to *M. arizonicum* in gynostegium structure.

Taxonomic History

The genus *Metastelma*, established by Robert Brown (1810), is based on *M. parviflorum*, and initially included only that species. During the next 130 years numerous species were added from all over the Americas, most of them corresponding to the current concept of the genus. In the Caribbean Schlechter (1899) included *Amphistelma* Griseb. and *Orthosia* in *Metastelma*, but in Central and South America, *Orthosia* remained distinct. Woodson (1941) sank all North American Asclepiadeae into only eight genera, *Asclepias* L., *Blepharodon* Decne., *Cynanchum* L., *Fischeria* DC., *Gonolobus* Michx., *Matelea* Aubl., *Oxypetalum* R. Br., and *Sarcostemma* R. Br. While Woodson's (1941) concept was useful for the fast naming of the many asclepiads emerging during expeditions to Central and South America, and was therefore readily adopted, careful re-examination has shown that some of the enlarged genera are highly artificial—in particular *Sarcostemma* (Liede, 1996a; Liede & Täuber, 2000) and *Cynanchum* (Liede & Täuber, 2002; Liede & Kunze, 2002). For *Metastelma*, Woodson (1941) stated that he did not know the genus well enough to carry out the numerous necessary name changes, a task readily carried out in the course of the various floras published after 1941 (see above). Stevens (1988) reverted to considering *Metastelma* as a distinct genus, though without arguing his case in detail. Like Schlechter (1899), Stevens (1988) did not consider *Orthosia* distinct from *Metastelma*. The few floristic treatments published in the area after 1988 (Fishbein, 1998; Levin & Moran, 1989) follow this usage. Liede (1997) argued for a distinct genus *Orthosia* for morphological reasons, but did not propose any formal transfers. Stevens (2001) was the first to reestablish *Orthosia* in a flora treatment. Molecular results based on cpDNA (Liede & Täuber, 2002) are supporting *Metastelma* and *Orthosia* as distinct genera independent of *Cynanchum*.

Morphology of the Southwestern North American and Central American Species of *Metastelma*

Habit and Shoots

All *Metastelma* species are slender twiners that may extend over several cubic meters, spreading over bushes and small trees. As far as known, all species possess a stout woody rootstock, from which several basally often slightly woody main shoots originate. In contrast to the often ladder-like branching pattern of *Orthosia*, where both leaf axils sprout a side branch, branching in *Metastelma* is highly irregular, and side branches sprout from one leaf axil only. Shoots may be glabrous, glabrescent, or pubescent, and the trichomes can occur over the entire shoot, along two lines, or along a single line, the position of which changes at every node. Trichomes on all vegetative parts are simple, multicellular, and smooth. Indumentum terminology follows Hewson (1988) throughout.

Leaves

The leaves are always decussate; the blades are usually ovate to elliptic, more rarely obovate or linear. They bear one to three small glandular organs, colleters (e.g., Thomas & Dave, 1991) directly at the base of the adaxial side of the blade at the transition point between petiole and midrib. Leaves can be glabrous or pubescent. Most frequently, the midrib on the adaxial side of the blade is rather densely covered with trichomes, the margin is ciliate, while the adaxial leaf blade is glabrous.

Inflorescences

A single, always extra-axillary inflorescence is borne at each node of the floriferous part of the shoot. The inflorescences are 2- to 12-flowered, and in most cases sciadioidal ("pseudo-umbellate," Weberling, 1989) or only slightly cymose. Only *Metastelma pedunculare* has a distinctly cymose inflorescence, usually with a single dichasium at the base. *Metastelma pedunculare* is also the only species in which the peduncles regularly exceed 1 cm in length.

Flowers. The flowers, which are always borne on a pedicel to 5 mm long, are 5-partite as characteristic for the Asclepiadoideae. They are usually

nectariferous, but, as far as known, unscented, except for *M. stenomeres* and *M. schlechtendalii* var. *schlechtendalii*, for which a sweet to very sweet scent is reported (*Schipp 674* for *M. stenomeres*; *Davidse & Brant 32667*, *Saunders 740* for *M. schlechtendalii*). They are generally very small (corolla length not exceeding 4.5 mm), and some (*M. cuneatum*, *M. latifolium*, *M. minutiflorum*) tiny (corolla length not exceeding 2 mm). A rather surprising display is created by the simultaneous opening of many flowers per inflorescence and many inflorescences. In general, the flowers are either star-shaped (e.g., *M. barbigerum*), or campanulate (*M. arizonicum*), or almost tubular (*M. stenomeres*). The calyx is basally fused, with the lobes usually less than 1.5 mm long, but to 3 mm long and pronouncedly acute in *M. arizonicum* and *M. mexicanum*.

Corolla. The corolla is white, cream, yellowish, brownish, or greenish abaxially, but always white to cream adaxially. Characteristic for *Metastelma* are the usually densely indumented, sometimes bearded adaxial sides of the corolla lobes. Several different types of simple trichomes can be distinguished. Smooth, hispid, downwardly directed trichomes are found just above the tube in the center of the corolla lobe in most species (Fig. 1c). Long, slightly verrucose and soft trichomes may form the "beard" at the tip of the corolla lobes, e.g., *M. barbigerum* var. *barbigerum* and *M. pringlei* (Fig. 1d, e). Shorter, more strongly verrucose trichomes are found in the apical and marginal parts of corolla lobes of taxa without a distinct "beard," e.g., *M. barbigerum* var. *liesnerianum* (Fig. 1c).

Corona. The corona is of gynostegial origin, but can occasionally be fused basally to the corolla (*M. parviflorum*, *M. mexicanum*). In contrast to *Orthosia*, in which the corona is fused for at least one third of its length, it consists of free staminal parts only (Kunze, 1997). The corona is always white, and variation between species comes about by variable length in relation to gynostegium length, shape, and fleshiness, e.g., in *M. barbigerum*, the corona is about as long as the gynostegium (Fig. 1a), while it is considerably longer with its parts connivent over it in *M. pringlei* (Fig. 1b). Point and angle of attachment of the lobes are further distinguishing characters: in both *M. barbigerum* var. *barbigerum* and *M. pringlei* the corona lobes form a distinct hook at the point of attachment (Fig. 1a, b), while this hook is much less pronounced, e.g., in the other two varieties of *M. barbigerum* as well as in *M. schlechtendalii*.

Gynostegium. The gynostegium can be either sessile, or elevated by a stalk (Fig. 1a, b). In general asclepiad terminology, a stipe, a feature occasionally found in *Cynanchum*, is a stalk elevating the gynostegium, but not the corona, and a column, typical for the Asclepiadinae, is a stalk elevating both the gynostegium and the corona. In *Metastelma*, the corona can be attached to the base of the stalk (e.g., *M. parviflorum*), along the stalk (e.g., *M. eliasianum*, *M. barbigerum*, *M. arizonicum*), or directly underneath the gynostegium (e.g., *M. pedunculare*, *M. stenomeres*). While the terms "stipe" and "column" have been used in the descriptions according to their definitions, all intermediate states exist, so that the distinction is purely formal. The outline of the gynostegium is a useful character in species identification, especially for the large and variable *M. barbigerum* and *M. schlechtendalii* complexes. *Metastelma barbigerum* always has a conical gynostegium with inclined anthers (Fig. 1a), while *M. schlechtendalii* always displays a more or less cubical gynostegium with erect anthers. In the Yucatán, this character distinguishes even the short-stiped forms of *M. schlechtendalii* from *M. barbigerum* var. *veracruzense* and variety *liesnerianum*, in which the hook-shaped corona attachment and the corolla "beard" easily identifying the typical variety are often less well developed. The guide rail, formed by the anther wings of two adjacent anthers is as long as the anther proper, except for *M. schaffneri*, where it is slightly shorter. It consists of an outer and an inner ridge, with the inner ridge shorter than the outer one and strongly curved (Fig. 1f). Pollinaria are minute and therefore difficult to use for identification, even though the shape of corpuscula, caudicles, and pollinia are species-specific. The lower part of the style-head possesses a

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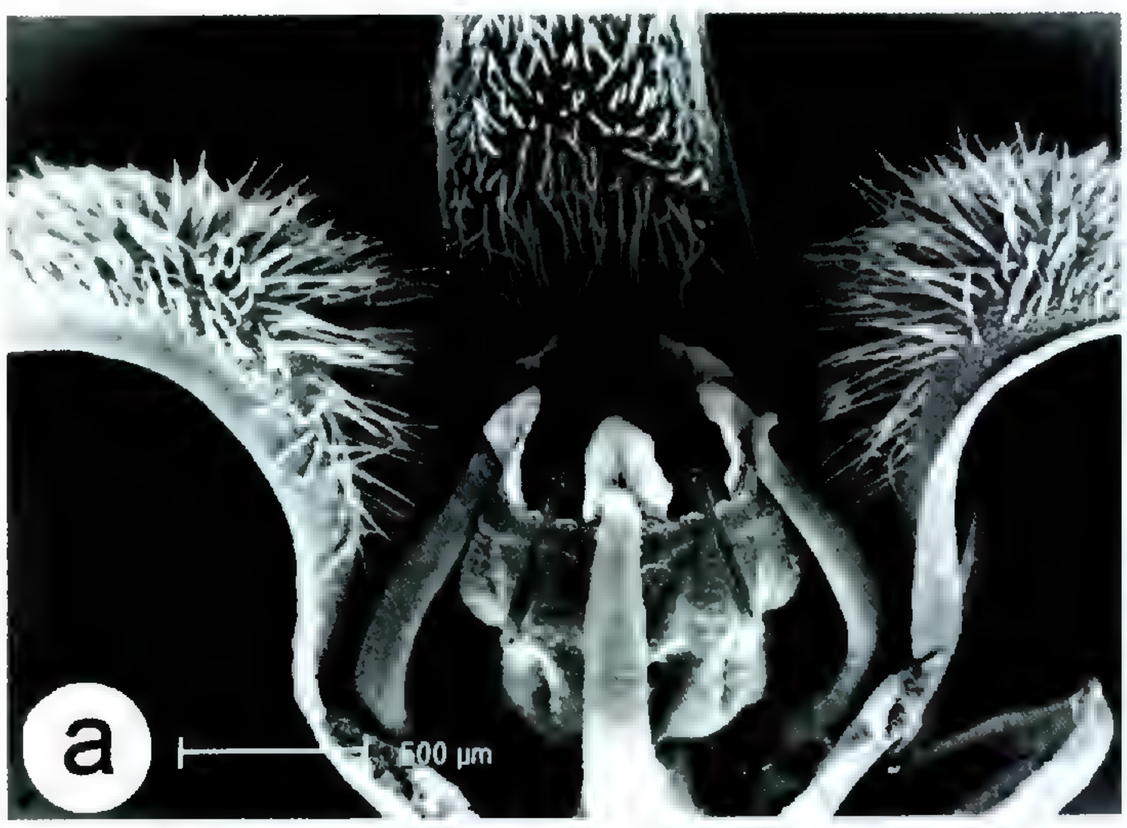
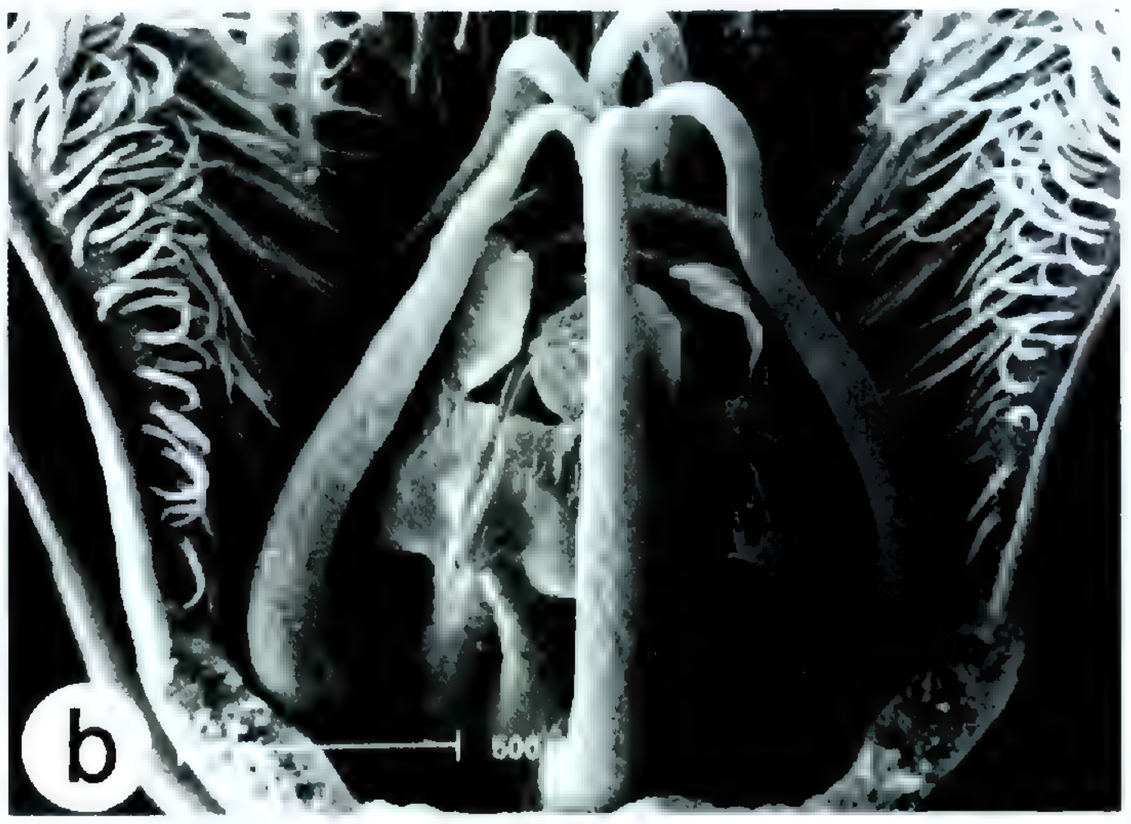
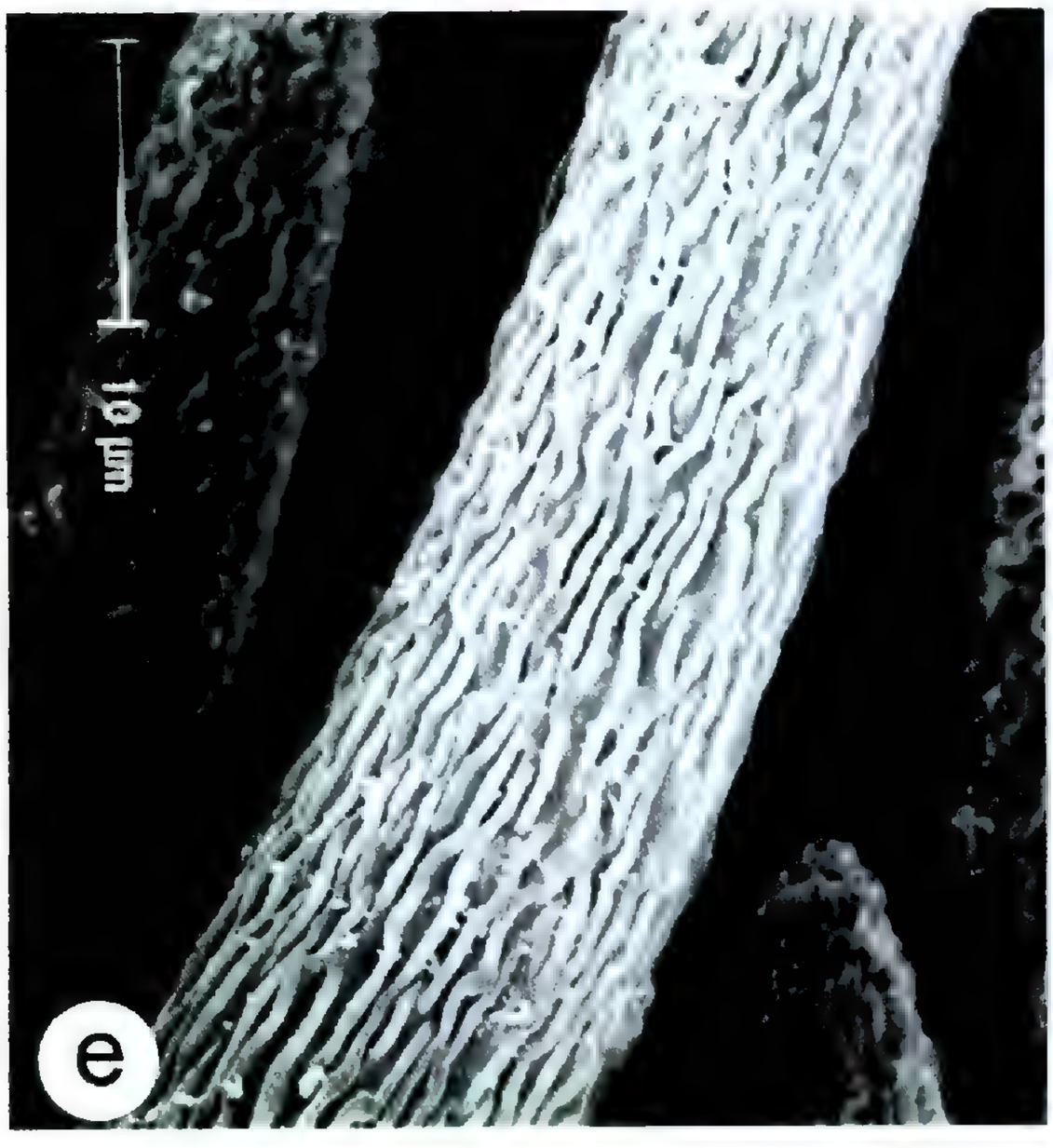
Figure 1. SEM studies of flowers and flower details. —a. *Metastelma barbigerum* var. *barbigerum*, flower in lateral view; two petals removed. —b. *Metastelma pringlei*, gynostegium with corona. —c. *Metastelma barbigerum* var. *liesnerianum*, upper regions of corolla lobe surface with smooth trichomes (center) and verrucose trichomes (margins). —d. *Metastelma pringlei*, simple, slightly verrucose trichomes on upper regions of corolla lobe surface. —e. *Metastelma barbigerum* var. *barbigerum*, detail of verrucose hair from median region of adaxial corolla lobe surface. —f. *Metastelma barbigerum* var. *barbigerum*, detail of gynostegium showing one anther with distal and proximal ridge (arrow) of anther wing and one pollinium with translator; one anther removed. a, e, f: *Liede & Conrad 2610*; b, d: *Liede & Meve 2501*; c: *Liede & Conrad 3242*.


a
500 µm


b
500

100 µm
c

50 µm
d


10 µm
e

10 µm
f

knob above the corpusculum and the upper part of the style-head is flat to conical in most cases. Only *M. mexicanum* can be easily recognized by its ob-infundibuliform style-head.

Follicles and seeds. One follicle per flower is generally developed. A compitum (Kunze, 1991) is thus absent. Follicles are slenderly obclavate to fusiform in shape, with a thin pericarp and without wings or other ornaments. Each follicle contains 10 to 20 seeds in an imbricate arrangement on the placenta. Seeds are ovate, oblong, or pyriform, winged or wingless, light to dark brown, glabrous or papillate, smooth, with longitudinal ridges or tuberculate, but no species with seed trichomes has been found.

CHROMOSOME NUMBERS

Of the species in western North and Central America, only *Metastelma barbigerum* var. *barbigerum* has been counted with $2n = 22$ (Albers et al., 1990, as *Matelea reticulata* (Gray) Woodson), the chromosome number found in more than 90% of all Asclepiadoideae (Albers & Meve, 2001).

HABITATS, DISTRIBUTION, PHENOLOGY, AND USES

Most Central American *Metastelma* species display a rather wide ecological amplitude and occur on various soils and in numerous vegetation types. *Metastelma arizonicum* subsp. *arizonicum* is a lowland desert scrub species, and *M. californicum* subsp. *californicum* occupies even drier habitats. Both taxa have a South or Central Mexican sister taxon living at higher altitudes and in forest habitats, open pine forests for *M. arizonicum* subsp. *chiapense* and tropical deciduous forests for *M. californicum* subsp. *lanceolatum*. Of the remaining Sonoran species, *M. cuneatum* and *M. minutiflorum* are restricted to the lowlands (to 200 m), where they inhabit thornscrub communities. *Metastelma latifolium* and *M. mexicanum* prefer altitudes above 200 m (to 1500 m) and live in open forest communities.

In Texas, *Metastelma barbigerum* var. *barbigerum* is commonly found in lowland areas (below 500 m), while *M. palmeri* prefers higher altitudes (above 500 m). In Mexico, though, *M. barbigerum* var. *barbigerum* is also found at higher altitudes to 2300 m, while the other two varieties are strictly lowland plants of sand dunes, rivers, and disturbed habitats. A similar difference in altitudinal preference characterizes the three subspecies of *M. schlechtendalii*. The typical variety is salt tolerant and occurs mainly in open or disturbed locations close to the sea, but is occasionally found as high as 2000 m in Guatemala. Morphologically extremely similar is the strictly coastal disjunct variety *arenicola*. Variety *trichophyllum*, easily recognized by its densely hispid leaves and more floriferous inflorescences, in contrast, prefers altitudes over 750 m and open forests. Other lowland species are *M. stenomeres*, a distinctive Belize endemic living in open pine forests, and *M. eliasianum*, extending from Panama to the west coast of South America (Colombia). The remaining four species, *M. longicoronatum*, *M. pedunculare*, *M. pringlei*, and *M. schaffneri*, occur regularly at altitudes between 1000 and 2500 m, although some specimens have been found as low as 500 m or as high as 2800 m. No *Metastelma*, however, was found above 3000 m. The latter four species, except for *M. pedunculare*, which has a weedy tendency, live in open forest habitats.

Very little is known about the reproductive and pollination biology in any species of the genus. Liede (unpublished) observed a small bee visiting *Metastelma californicum* subsp. *californicum*, and Fishbein (*Fishbein & McMahon 2769*, ARIZ) has observed bees, wasps, and flies (*Apis* sp., Halictidae, Sphecidae, and Diptera) on the same species. The host-plant index by Markku Savela, ⟨http://www.nic.funet.fi/pub/sci/bio/life/warp/food-plants-m.html⟩, lists *Metastelma* as probable host for the butterfly *Anetia thirza insignis* (Salvin, 1869) (Nymphalidae) in Panama and Costa Rica. Fruits have been observed in all but three species (*M. latifolium*, *M. longicoronatum*, *M. stenomeres*), but not to the extent suggesting that *Metastelma* belongs to the extremely rare asclepiads capable of self-fertilization, as e.g., *Tylophora hirsuta* Wight (Chaturvedi, 1988) and *Vincetoxicum nigrum* (L.) Moench (Lumer & Yost, 1995). The phenology data presented in the species descriptions are based on collections of these species over their entire range (see Appendices 1, 2; an index to scientific names is provided in Appendix 3). While most species show a distinct peak of flowering at a single locality, this peak may shift with changing geographical parameters. Also, most species continue to produce a few flowers after their peak flowering time is long past.

Metastelma is not generally noted among the recognized useful plants. Morton (1981: 692) noted, "Indians of Yucatán boil the root and repeatedly rinse the mouth with the decoction to heal canker sores. They warn that the decoction must not be swallowed."

TAXONOMY

Metastelma R. Br., Asclepiadeae: 41. 1810. TYPE: *Metastelma parviflorum* (Swartz) R. Br. [= *Cynanchum parviflorum* Swartz].

Acrocoryne Turcz., Bull. Soc. Imp. Naturalistes Moscou 25(2): 316. 1852. TYPE: *Acrocoryne caribaea* Turcz.

Basistelma Bartlett, Proc. Amer. Acad. Arts 44: 631. 1909. TYPE: *Basistelma mexicanum* (Brandegee) Bartlett [= *Melinia mexicana* Brandegee], lectotype, designated here.

Decastelma Schltr., in Urban, Symb. Antill. 1: 264. 1899. TYPE: *Decastelma broadwayi* Schltr.

Epicion Small, Fl. Miami 149. 1913. Type: *Epicion bahamense* (Griseb.) Small (*Metastelma bahamense* Griseb.).

Irmischia Schldl., Linnaea 19: 738. 1847. TYPE: *Irmischia floribunda* Schldl.

Meresaldia Bullock, Kew Bull. 19: 203. 1965. *Esmeraldia* E. Fourn., Ann. Sci. Nat. Bot., sér. 6.14: 367–368. 1882, non *Esmeralda* Rchb. f., Xenia Orchid. 2: 38. 1862 (Orchidaceae). TYPE: *Meresaldia stricta* (E. Fourn.) Bullock [= *Esmeraldia stricta* E. Fourn.].

Stelmation E. Fourn., in Martius, Fl. Bras. 6(4): 226. 1885. TYPE: *Stelmation myrtifolium* (Decne.) E. Fourn. [= *Metastelma myrtifolium* Decne.].

Plants small, slender twiners, to 400 cm high, richly irregularly branched; *subterranean organs* constituting a woody rootstock; *shoots* herbaceous, basally often slightly woody or corky, pubescent, glabrescent or glabrous; *latex* white to ivory; pseudostipules (extremely reduced short shoots with a pair of smaller and sometimes differently shaped leaves) absent. *Leaves* opposite, petiolate, with 0 to 3 colleters at blade base; blades herbaceous. *Inflorescences* usually one per node, extra-axillary, 2- to 12-flowered, bostrychoid or sciadioidal, peduncule to sessile; *floral bracts* present, triangular or ovate. *Floral buds* elongated-conical, conical, ovoid or cylindrical; *calyx* basally fused, campanulate, lobes ovate, acute to acuminate; *corolla* rotate to campanulate to almost tubular, 1.5–4.5 mm long, abaxially white, cream, yellow, green, or brown, glabrous, adaxially white, densely covered with verrucose and smooth trichomes, arranged in species-specific patterns; *gynostegial corona* of free staminal lobes, white, glabrous; lobes simple. *Gynostegium* sessile or atop a stipe or a column; *anther wings* consisting of distal and proximal ridge, proximal ridge short, curved; *connective appendages* present, ovate or triangular; *pollinarium* with two pollinia per pollinarium, (sub)apically attached to the caudicles, pendulous, not possessing a germination pore; *upper part of the style-head* depressed-conical to conical, rarely flat or elongated-conical. *Follicles* one, occasionally two per flower, 25–80 mm long, obclavate or fusiform, terete or obtusely deltate in cross section, apically beaked, wingless, slightly longitudinally grooved, usually glabrous, with thin pericarp; *seeds* 4–7 mm long, brown, winged or wingless, glabrous or papillose, smooth or with longitudinal ridges or tuberculate, without trichomes, comose.

Chromosome number. $2n = 22$ (*Metastelma barbigerum* var. *barbigerum*, Albers et al. (1990), as *Matelea reticulata* (Gray) Woodson).

Basistelma was created by Bartlett (1909) to accommodate two species, *B. angustifolium* (Torr.) Bartlett and *B. mexicanum* (Brandegee) Bartlett, that are at first glance ill fitted in *Metastelma* because of their long, conspicuous style-head. Fishbein and Levin (1997) correctly included *Basistelma* in *Metastelma*, and recognized the two former *Basistelma* species as identical. As the basionym of *B. angustifolium*, *Metastelma angustifolium* Torr., is a homonym of *Metastelma angustifolium* Turcz. (a taxon belonging to the genus *Orthosia*) and thus not a name available in *Metastelma*, Fishbein and Levin (1997) assigned the name *Metastelma mexicanum* (Brandegee) Fishbein & Levin to this species. Under these circumstances, it is logical to select *Basistelma mexicanum* as the lectotype of *Basistelma*, an action not carried out by Fishbein and Levin (1997).

Key to the Species of *Metastelma* in the Southwestern U.S.A. and Central America*

1a. Gynostegium sessile or almost so.
  2a. Flowers tiny; corolla lobes not longer than ca. 2 mm (northern Pacific slope of Mexico only).
    3a. Corolla lobes puberulent with very short trichomes (< 0.1 mm long); corona distinctly laminar, at least basally as broad as the anthers ..... 4. *M. cuneatum*
    3b. Corolla lobes densely covered with longer trichomes (> 0.1 mm long); corona lobes ± subulate, distinctly smaller than the anthers.
      4a. Leaves linear to very slenderly lanceolate, shoots with two lines of trichomes, inflorescences subsessile, pollinia reniform, style-head conical ..... 9. *M. minutiflorum*
      4b. Leaves ovate, apiculate, shoots with one line of trichomes, inflorescences with a peduncle 2–4 mm long, pollinia ovoid to oblongoid, but not reniform, style-head flat ... 6. *M. latifolium*
  2b. Flowers larger; corolla at least 2.5 mm long ..... 3. *M. californicum*
    5a. Base of staminal corona lobes smaller than the anthers; plants of northern Mexico ..... 3a. *M. californicum* subsp. *californicum*
    5b. Base of staminal corona lobes at the base broader than the anthers; plants of central and southern Mexico ..... 3b. *M. californicum* subsp. *lanceolatum*
1b. Gynostegium with a distinct stipe.
  6a. Stipe as long as the gynostegium or shorter than it.

7a. Corona distinctly shorter than the gynostegium; anther appendages about twice as long as the anthers, erect; style-head with a pronounced appendage; corolla lobes apically with very short (< 0.05 mm long) verrucose trichomes (giving a papillose appearance) and a tuft of smooth, stiff trichomes at the base of each corolla lobe ..... 8. *M. mexicanum*

7b. Corona as long as or longer than the gynostegium; anther appendages not longer than the anthers, inflexed; style-head without a pronounced appendage; corolla lobes apically with distinct trichomes (at least 0.1 mm long) and smooth trichomes, if present, not restricted to a small tuft.

8a. Corona ca. 1.5 mm long, about twice as long as the gynostegium, including stipe, concealing the gynostegium ..... 12. *M. pringlei*

8b. Corona shorter than 1.5 mm, 1.5 times as long as the gynostegium (incl. stipe) or less, not concealing the conical gynostegium.

9a. Corona distinctly lanceolate, suddenly broadening at the base, producing an almost hastate shape ..... 7. *M. longicoronatum*

9b. Corona never suddenly broadening at the base to produce a hastate shape.

10a. Corona attached along the stipe, lobes subulate and bases hardly broader than apex or slenderly ovate to lanceolate, with or without a long extended tip, often attached to the stipe with a pronounced hook.

11a. Corona attached to the stipe with a pronounced hook, lobes longer than 1 mm and style-head longer than 0.5 mm.

12a. Stems and pedicels with a single line of recurved trichomes; calyx with a few sparse trichomes; leaves less than 3 mm wide; corolla lobes oblong or ovate, but not apically suddenly narrowing; trichomes of the adaxial side of the corolla lobes apically not distinctly longer than laterally ..... 1. *M. arizonicum*

13a. Stems basally often corky, leaf veins with trichomes; calyx lobes very slenderly ovate, almost as long as the corolla lobes, but at least reaching half of corolla length; corolla lobes adaxially laterally and apically with long (0.2–0.3 mm), distantly verrucose trichomes; plants of the southwestern U.S.A. and northern Mexico ..... 1a. *M. arizonicum* subsp. *arizonicum*

13b. Stems basally never corky, leaf veins glabrous, calyx lobes ovate, not very slender and not reaching half of corolla length; corolla lobes adaxially apically and laterally with short (ca. 0.1 mm), strongly verrucose trichomes; plants of southern Mexico, Guatemala, Honduras ..... 1b. *M. arizonicum* subsp. *chiapense*

12b. Stems, pedicels, and calyx glabrous, corolla lobes ovate to lanceolate, often apically rather abruptly narrowing; trichomes of the adaxial side of the corolla lobes apically distinctly longer than laterally ..... 2a. *M. barbigerum* var. *barbigerum*

11b. Corona ± flatly attached underneath the gynostegium, either lobes shorter than 1 mm or style-head shorter than 0.5 mm, or both.

14a. Pedicels glabrous; stems glabrous or with a single line of trichomes, calyx with a few isolated trichomes on the tube ..... 2b. *M. barbigerum* var. *liesnerianum*

14b. Pedicels densely covered with trichomes; stems always with a single, occasionally very broad line of trichomes; calyx with trichomes ..... 2c. *M. barbigerum* var. *veracruzense*

10b. Corona attached directly underneath the gynostegium, lobes ovate to triangular, always without a long extended tip, never attached to the stipe with a pronounced hook.

15a. Leaves, at least those of flowering branches, mostly linear or lanceolate, rarely ovate; corona lobes not distinctly flat, oblong, considerably exceeding the flatly cylindrical gynostegium ..... 13. *M. schaffneri*

15b. Leaves normally ovate; corona lobes distinctly flat and much broader at the base than at the apex, barely exceeding the slightly conical gynostegium.

16a. Trichomes of the adaxial side of the corolla apically and laterally of equal length and fairly short (0.1–0.15 mm); leaves narrowly ovate, on flowering branches not exceeding 15 mm long; corolla usually less than 2.5 mm (rarely to 3 mm) long ..... 10. *M. palmeri*

16b. Trichomes of the adaxial side of the corolla apically slightly longer than laterally (to 0.2 mm); leaves ovate, on flowering branches to 25 mm long; corolla to 4 mm long ..... 16. *M. turneri*

6b. Stipe distinctly longer than the gynostegium.

17a. Corolla fused at least for a quarter of total length.

18a. Corona attached to the stipe immediately below gynostegium.

19a. Corona almost twice as long as the gynostegium without stipe; style-head conical;

leaves slenderly elliptic or lanceolate; peduncle 3–5 mm long; inflorescences sciadioidal; floral bracts glabrous ..... 15. *M. stenomeres*

19b. Corona just exceeding the gynostegium; style-head flat; leaves ovate; peduncle at least 10 mm long; inflorescences bostrychoid; floral bracts ciliate ..... 11. *M. pedunculare*

18b. Corona not attached immediately below gynostegium.

20a. Corona clearly attached to stipe; corolla fused for less than half of its length, lobes with dense, almost woolly trichomes; stipe stout, not more than twice as long as the gynostegium; plants of Central and South America ..... 5. *M. eliasianum*

20b. Corona attached to the corolla; corolla fused for half of its length or more, lobes with sparse, short pubescence; stipe very slender, at least three times as long as the gynostegium; plants of South America ..... *M. parviflorum* R. Br.*

17b. Corolla fused only basally (corona attached along stipe) ..... 14. *M. schlechtendalii*

21a. Adaxial leaf surface with evenly spread trichomes; inflorescences usually with more than 6 flowers; pedicels with evenly distributed trichomes ..... 14c. *M. schlechtendalii* var. *trichophyllum*

21b. Adaxial leaf surface (except for midrib) without trichomes; inflorescences usually with less than 6 flowers; pedicels with a single line of trichomes or glabrous.

22a. Inflorescences distinctly pedunculate, peduncles normally more than 4 mm long; floral bracts and sepals ovate; corona exceeding the gynostegium by less than gynostegium length; style-head flat to slightly umbonate ..... 14a. *M. schlechtendalii* var. *schlechtendalii*

22b. Inflorescences subsessile, peduncles less than 4 mm long; floral bracts and sepals distinctly lanceolate; corona exceeding the gynostegium by as much as or more than gynostegium length; style-head distinctly umbonate ..... 14b. *M. schlechtendalii* var. *arenicola*

**Metastelma parviflorum* is not treated here in detail, but is included in the key because it is widespread in the Caribbean and South America, and the name has often been applied to material of *M. schlechtendalii*.

1. Metastelma arizonicum A. Gray, Proc. Amer. Acad. Arts 19: 85. 1883. *Cynanchum arizonicum* (A. Gray) Shinners, Sida 1: 365. 1964. TYPE: U.S.A. Arizona: Pima Co., hills near Tucson, 22 May 1883, *C. G. Pringle 20* (holotype, GH not seen). Figures 2a–h, 3.

1a. Metastelma arizonicum A. Gray subsp. **arizonicum**

Metastelma watsonianum Standl., Contr. U.S. Natl. Herb. 23: 1175. 1924. Basionym: *Metastelma albiflorum* S. Watson, Proc. Amer. Acad. Arts 24: 60. 1889, non *Metastelma albiflorum* Griseb., Fl. Brit. W. Ind.: 417. 1862. TYPE: Mexico. Sonora: Guaymas, *E. Palmer 223* (holotype, GH not seen; isotypes, NY—2!).

Plants ascending, 80–250 cm high; *shoots* perennial, basally corky, isolatedly to sparsely covered along a single line with recurved trichomes, ca. 250–300 μm long; internodes 1–4 cm long, ca. 1 mm diam. *Leaves* with petioles 1–2 mm long, with 1 or 2 colleters at blade base; blades 10–20 × 1.5–3 mm, elliptic to ovate, basally rounded to cuneate, apically acute to acuminate, marginally straight or revolute (when dry), adaxially and abaxially glabrous, but sparsely covered on the midvein and margins with recurved trichomes, 200–250 μm long. *Inflorescences* always one per node, 1- to 4-flowered, 1 to 4 flowers open synchronously, sciadioidal, subsessile; *floral bracts* 1–1.5 × 0.2–0.5 mm at the base, deltoid, slightly papillose and with trichomes on the surface; *pedicels* 1–2 mm long, sparsely covered over the entire surface with recurved trichomes, 200–250 μm long. *Floral buds* 2.5–3 mm long, 1–1.5 mm diam., ovoid, with imbricate aestivation; *calyx* basally fused, campanulate, abaxially vaguely glandular, with a few sparse trichomes; calyx lobes 2–2.5 × 0.3–0.5 mm, very slenderly ovate, apically acute; *corolla* campanulate, 2.5–4 mm long, white, abaxially glabrous, adaxially with distantly verrucose trichomes, 200–300 μm long, on the apical and on the lateral parts of the lobes and with downward-directed, hispid trichomes, 300–500 μm long, on central part of the lobes at the mouth of the tube; lobes fused for ca. ¼ of total corolla length, 1 mm wide, patent and recurved, apically acute; *gynostegial corona* 1.5–2 mm long, equaling to longer than the gynostegium; lobes inflexed or apically reflexed, attached at the base of the stipe with a distinct hook-shaped base, laminar to solid, subulate. *Gynostegium* ca. 1.5 mm high, ca. 0.7 mm diam., on a stipe 0.7 mm long; *anthers* about as high as broad, deltoid, abaxially convex; anther wings ca. 500 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther to slightly centrifugal; connective appendages ca. 400 μm long, ca. 250 μm wide, triangular, equaling the stamen in width, erect; *pollinarium* with corpusculum 150 μm long, more than twice as long as broad, elliptic; caudicles 80 μm long, cylindrical, s-shaped, convex-concave; pollinia subapically attached to the caudicles, 200–

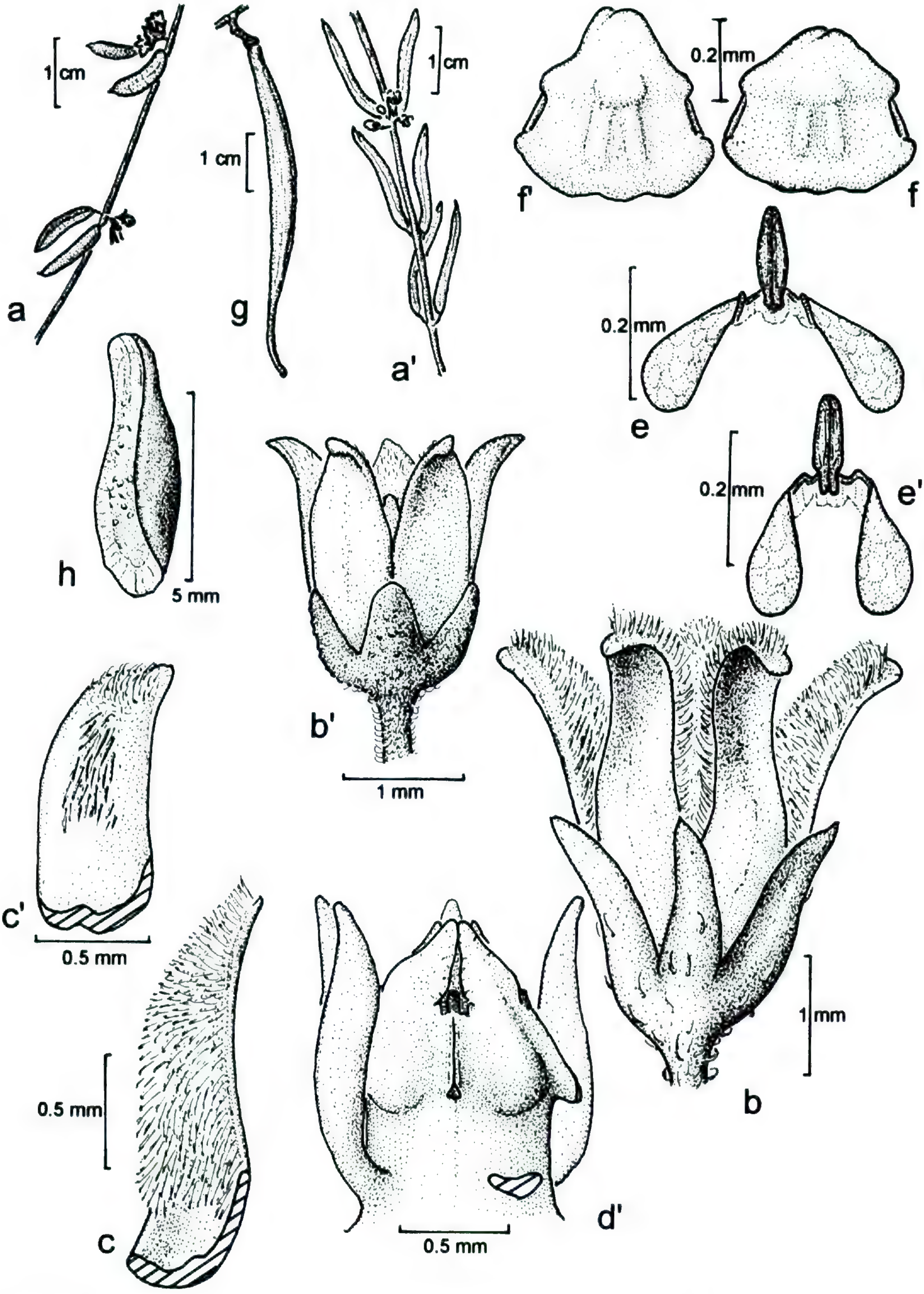


Figure 2. *Metastelma arizonicum*. a–h. *Metastelma arizonicum* subsp. *arizonicum*. a′–f′ *Metastelma arizonicum* subsp. *chiapense*. —a, a′. Habit. —b, b′. Flower. —c, c′. Corolla lobe, adaxial view. —d′. Corona and gynostegium. —e, e′. Pollinarium. —f, f′. Style-head. —g. Follicle. —h. Seed. a–c, e, f: *Steinmann & Varela 972*. g, h: *Neese & Neese 10076*. a′: *Ghiesbreght 664*. b′–f′: *Liede & Conrad 2559*. Drawn by J. Conrad.

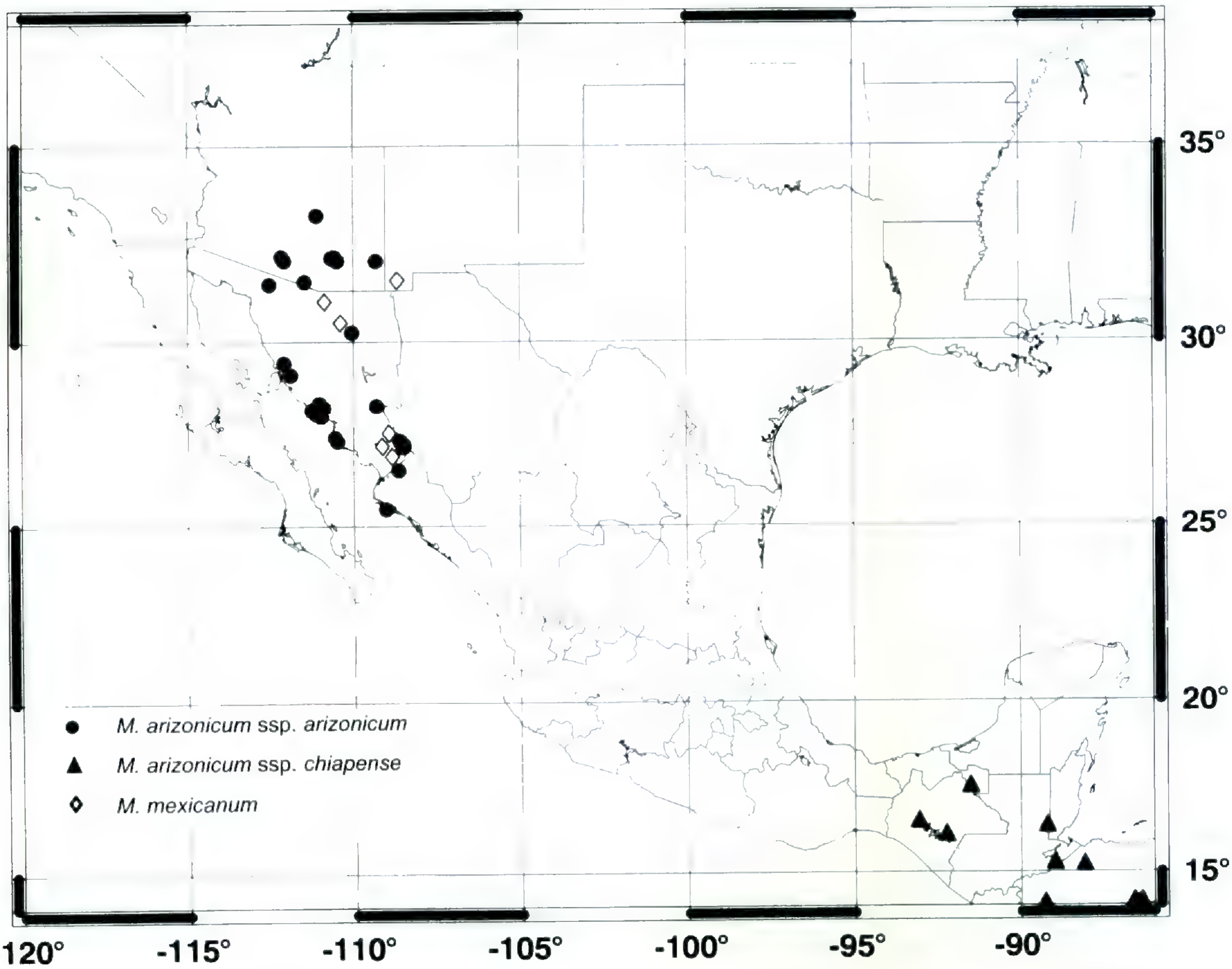


Figure 3. Distribution of *Metastelma arizonicum* and *M. mexicanum*.

220 μm long, 80 μm wide, ovate in cross section, clavate; *style-head* white, 0.4 mm diam., 0.5 mm high, upper part 0.2 mm high, shorter than to equaling the lower part, depressed-conical to conical. *Follicles* always one per flower, pendulous, 45–65 mm long, 3–4 mm diam., fusiform, terete, apically strongly beaked, medium to dark brown, glabrous; *seeds* ca. 10 per follicle, 5–6 mm long, 2–3 mm wide, pyriform, medium brown, seta and aseta side tuberculate, marginally with 0.15 mm wide wing with entire margin; coma 20–30 mm long.

Phenology. Collected in flower in April, June, and from August to January; in fruit from March to May and September to January.

Distribution. Mexico: Sonora; U.S.A.: Arizona; mostly on rocky slopes in desert scrub communities; 10–1000 m.

Literature and illustrations. Wiggins (1940: 82, pl. 18).

Additional specimens examined. MEXICO. **Sonora:** ca. 8.3 rd. mi. N of Arizpe on MEX Hwy. 2, 1 Sep. 1996 (fl, fr), *Shortman 96-27* (ARIZ); Arroyo El Mentidero, 11.3 km S of Alamos, 25 Nov. 1993 (fl, fr), *Van Devender et al. 93-1310* (ARIZ); near Arroyo Grambullo on NE side of Rio Yaqui bridge on Mex 16, 15 Sep. 1998 (fl), *Van Devender & Reina 98-1132* (ARIZ); rd. to Bahia San Carlos, 12 Jan. 1965 (fl), *Thomas & Felger 11942* (ARIZ); ca. 1 mi. N of Bahia San Carlos on rd. to Algodones, 24 Nov. 1963 (fl), *Felger 9579* (ARIZ); Bahía Colorado, E side of Morro Colorado, 28 Dec. 1966 (fl, fr), *Felger 15588* (ARIZ); Bahia de San Pedro, Sep. 1954 (fl, fr), *Turner et al. 79-261* (ARIZ); ca. 5 km E of Bahia San Pedro, 17 Nov. 1984 (fl), *Felger & Zamulio 84-461* (ARIZ, LL); Canon la Pintada, 3 Jan. 1984 (fl, fr), *Van Devender & Van Devender et al. 84-29* (ARIZ); Cerro de la Vigia, Guaymas, ± 380 m, 9 Jan. 1965 (fl), *Thomas & Felger 11785* (ARIZ); Cerro de Navachiste about Bahia Topolobampo, Sep. 1954 (fl, fr), *Gentry 14304* (ARIZ, LL); Cerro del Viejo SW of Caborca, 9–11 Oct. 1954 (fl, fr), *Gentry 14466* (ARIZ); 23 mi. S of Divisadero, 26 Sep. 1934 (fl), *Wiggins 7491* (ARIZ); El Baviso, ca. 2.5 km NE of Bahia San Carlos, 18 Nov. 1984 (fl), *Felger & Zamulio 84-490* (ARIZ); Enseñada Chica ca. 23 km N, 39 km W of Guaymas, 1 Oct. 1979 (fl, fr), *Burgess 5695* (ARIZ); Enseñada Grande [= Bahia San Pedro], 11 Nov. 1964 (fl), *Russell et al. 11402* (ARIZ); Guajaray, Rio Mayo, 23 Oct. 1934 (fl), *Gentry 1098* (ARIZ); Guaymas, *Palmer 626* (NY); 2 km E of MEX 15 on rd. to Microondas Las Avispas, 21 Sep. 1997 (fl), *Reina et al. 96-286* (ARIZ); 1 km E of Los Camotes, along Los Tanques–Las Chinacas rd., 18 Aug. 1994, *Fishbein et al. 1878* (ARIZ); San Bernardo, Rio

Mayo, 12 Feb. 1935 (fl), *Gentry 1298* (ARIZ); Sierra Cipriano, 28 Apr. 1991 (fl, fr), *Felger & Quijada-Mascarenas 91-33* (ARIZ); Sierra Libre, ca. 2 km E of the junction with MEX 15, 2 Sep. 1996 (fl), *Steinmann & Varela 972* (ARIZ, NY); Sierra Seri, Hast Eemla, 17 Apr. 1974 (fl, fr), *Drees et al. 74-15* (ARIZ). U.S.A. **Arizona:** Pima Co., Baboquivari Mts., N of guest house, 8 Oct. 1944 (fl, fr), *Gould et al. 2804* (NY); Baboquivari Mts., Fresnal Canyon, 7 Sep. 1931 (fl), *Gilman 140* (NY); Quiotoa Mts., 19 Oct. 1945 (fl), *Goodding 208-45* (NY); 3.5 mi. below Molino Basin Campground, Santa Catalina Mts., 18 Apr. 1969 (fl, fr), *Keil 4323* (NY); Santa Catalina Mts., 21 Dec. 1895 (fl, fr), *Tourney s.n.* (NY); Sierra Tucson, 26 May 1884 (fr), *Pringle s.n.* (NY, topotype); Ventana Park, E of San Miguel, 13 Oct. 1945 (fl, fr), *Goodding 116-45* (NY). Pinal Co., Superstition Mts., milepost 206, Hwy. 88, ca. 20 mi. E of Phoenix, 14 Apr. 1981 (fl, fr), *Neese & Neese 10076* (NY). County not known: 28 Apr. 1884 (fl, fr), *Le Roy s.n.* (NY); Sonora, 15. Aug. 1884 (fl), *Pringle s.n.* (NY).

1b. Metastelma arizonicum A. Gray subsp. **chiapense** (A. Gray) Liede & Meve, comb. et stat. nov. Basionym: *Metastelma chiapense* A. Gray, Proc. Amer. Acad. Arts 21: 397. 1886. *Cynanchum chiapense* (A. Gray) Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 226. 1947. TYPE: Mexico. Chiapas: 1864–1870, *A. B. Ghiesbreght 664* (holotype, F (neg. 059661)!; isotypes, GH not seen, MO not seen, NY!). Figures 2a′–f′, 3.

Metastelma collinum S. F. Blake, Contr. U.S. Natl. Herb. 24: 19. 1922. *Cynanchum collinum* (S. F. Blake) Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 226. 1947. TYPE: Guatemala. Izabal: trail from Los Amates to Izabal, 31 May 1919, *S. F. Blake 7793* (holotype, US-989629!; isotypes, GH not seen, US not seen).

Plants ascending, ca. 50 cm high, richly basitonically to irregularly branched. *Subterranean organs* constituting a woody rootstock; *shoots* perennial, sparsely covered along a single line with recurved trichomes, 200–250 μm long; internodes 1.5–5.5 cm long, 0.5–1 mm diam. *Leaves* with petioles 1–2 mm long, with 1 or 2 colleters at blade base; blades 15–35 × 1.5–3 mm, linear, elliptic, or ovate, basally rounded to cuneate, apically acute to acuminate, adaxially and abaxially glabrous, but marginally sparsely ciliate. *Inflorescences* one, occasionally two per node, 3- to 7-flowered, 3 to 5 flowers open synchronously, sciadioidal, sessile to subsessile; *floral bracts* 0.6–1 × 0.3–0.5 mm at the base, ovate; *pedicels* 1–3 mm long, sparsely covered over the entire surface with recurved trichomes, 100–150 μm long. *Floral buds* 1.8–2.2 mm long, 1–1.5 mm diam., ovoid; *calyx* basally fused, rotate to campanulate, abaxially vaguely glandular and with a few sparse trichomes; calyx lobes 1–1.5 × ca. 0.5 mm, ovate, apically acute; *corolla* campanulate, 2–2.5 mm long, abaxially and adaxially white, abaxially glabrous, adaxially with verrucose trichomes, ca. 100 μm long, on the apical and on the lateral parts of the lobes and with smooth, downward-directed trichomes, 300–400 μm long, on the central parts of the lobes; lobes fused for ca. ⅓ of total corolla length, 0.8–1.2 mm wide, erect, apically recurved, ovate, apically acute; *gynostegial corona* 1.2–1.5 mm long, equaling the gynostegium; lobes slightly inflexed, attached at the base of the stipe with a distinct hook-shaped base, laminar to filiform, oblong, with entire margins. *Gynostegium* ca. 0.8 mm high, ca. 1 mm diam., on a stipe 0.6 mm long; *anthers* about as high as broad, deltoid, abaxially convex; anther wings ca. 300 μm long, anther wings of adjacent anthers parallel to each other, centrifugal; connective appendages ca. 400 μm long, ca. 300 μm wide, ovate, equaling the stamen in width, slightly inflexed; *pollinarium* with corpusculum 150 μm long, more than twice as long as broad, elliptic; caudicles 70 μm long, cylindrical, slightly s-shaped, convex-concave; pollinia apically to subapically attached to the caudicles, 200–220 μm long, 80 μm wide, ovate in cross section, clavate; *style-head* white, 0.5 mm diam., 0.5 mm high, upper part 0.25 mm high, depressed-conical to conical. *Follicles* and *seeds* unknown.

Phenology. Collected in flower in April, May, July, and from September to November.

Distribution. El Salvador: Santa Ana; Guatemala: Péten; Honduras: Morazán; Mexico: Chiapas; rocky slopes, very open pine forests; 650–1700 m.

Metastelma arizonicum, *M. barbigerum*, and *M. pringlei* form a group of closely related species. They share bearded corolla lobes, the conical shape of the gynostegium, and the protruding anther wings. Yet, they are relatively easily separated by the length of the corona lobes (ca. 1.5 mm long, about twice as long as the gynostegium in *M. pringlei*, shorter than 1.5 mm and at the most 1.5× as long as the gynostegium in *M. arizonicum* and *M. barbigerum*) and the more slender shape of the gynostegium of *M. arizonicum* compared to *M. barbigerum*. *Metastelma arizonicum* and all varieties of *M. barbigerum* except variety *veracruzense* have distinctly clavate pollinaria, while those of *M. pringlei* are ovoid. In *M. arizonicum* subsp. *arizonicum* and *M. pringlei* strongly verrucose trichomes on the corolla lobes are absent, while they are present in subspecies *chiapense* as well as in *M. barbigerum*.

Despite the relatively wide distribution gap between the two subspecies of *M. arizonicum* (Fig. 3), the morphological differences between the taxa are rather inconspicuous, mainly concerning size dif-

ferences and variation in indumentum density on leaves and calyx, as well as the presence of strongly verrucose trichomes on the corolla lobes (present in subsp. *chiapense*, absent in subsp. *arizonicum*).

Additional specimens examined. EL SALVADOR. **Santa Ana:** vicinity of Santa Ana, 28–30 June 1922 (fl), *Standley 20418* (NY). GUATEMALA. **Petén:** Dolores, about 3 km NWW of village, 18 Oct. 1961 (fl), *Contreras 3068* (LL). HONDURAS. **El Paraíso:** Río Dantas, 5 July 1962 (fl), *Webster 12045* (MO). **Morazán:** entre Las Mesas y Guayabillas, 5 km empalme carretera Danlí–Yuscarán, 4 Nov. 1963 (fl), *Molina 13162* (LL, NY); entre km 11–12 carretera Suyapa a La Montañita, 11 Sep. 1963 (fl), *Molina 12851* (NY). MEXICO. **Chiapas:** Cerro del Ocote, 30 km NW of Ocozocoautla, 14 Oct. 1972 (fl), *Breedlove 28986* (NY); La Cienega de Leon, 30 km N of Las Cruces, 30 Nov. 1980 (fr), *Breedlove 48083* (MO); Comitán de Dominguez, 21 July 1989 (fl), *Liede & Conrad 2559* (UBT); Hacienda Monserrate, *Purpus 9078* (NY). **Oaxaca:** Cerro de Picardo, July 1914 (fl), *Purpus 7273* (NY).

2. Metastelma barbigerum Scheele, Linnaea 21: 760. 1848. *Cynanchum barbigerum* (Scheele) Shinners, Field & Lab. 19: 65. 1951. TYPE: U.S.A. Texas: Comal Co., New Braunfels, Aug. 1846, *F. Lindheimer 459* (lectotype, designated by Blankinship (1907: 143), MO; isotypes, GH not seen, NY!). Figures 4a–i, 5.

2a. Metastelma barbigerum var. **barbigerum**

Plants ascending, 30–80 cm high; *shoots* annual, glabrous. *Leaves* with petioles 2–8 mm long, with 0 to 2 colleters at blade base; blades 10–40(–60) × 3–14(–20) mm, ovate, basally rounded, apically acute, or rarely shortly acuminate, adaxially isolatedly covered mainly on veins and margins with flexuous to recurved trichomes, 250–300 μm long, abaxially glabrous. *Inflorescences* always one per node, 2- to 6-flowered, 2 to 5 flowers open synchronously, sciadioidal, subsessile to sessile; *floral bracts* 0.6–0.8 × ca. 0.2 mm at the base, ovate; *pedicels* 4–6 mm long, glabrous. *Floral buds* 3–3.5 mm long, 1–1.5 mm diam., conical to elongated-conical; *calyx* basally fused, rotate to campanulate, abaxially glabrous; calyx lobes 0.8–1.2 × 0.5–0.7 mm, ovate, apically acute; *corolla* 3.2–5.2 mm long, abaxially white to cream (when dry), glabrous, adaxially white, with slightly verrucose trichomes, 200–500 μm long, forming a woolly beard on the apical parts of the lobes and downward-directed hispid stiff trichomes, 300–500 μm long, on the central parts of the lobes; lobes fused to ca. ⅓ of total corolla length, 0.8–1 mm wide, straight, erect, oblong to lanceolate, apically often rather abruptly narrowing, acute, recurved, occasionally twisted; *gynostegial corona* 1–1.3 mm long, equaling to longer than the gynostegium; lobes erect to inflexed, attached at the base of the stipe with a distinct hook-shaped base, laminar to solid, subulate. *Gynostegium* 0.7–0.9 mm high, 1–1.2 mm diam., on a stipe 0.5–0.7 mm long; *anthers* about as high as broad, trapezoidal, abaxially planar; anther wings 400 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, centrifugal; connective appendages 200–300 μm long, 200–300 μm wide, equaling the stamen in width, slightly inflexed; *pollinarium* with corpusculum 400 μm long, between 1.5 times and twice as long as broad, ovoid; caudicles 250 μm long, cylindrical, geniculate; pollinia apically attached to the caudicles, ca. 400 μm long, 250 μm wide, ovate in cross section, clavate; *style-head* white, ca. 0.8 mm diam., 0.5 mm high, upper part 0.25 mm high, equaling the lower part, depressed-conical. *Follicles* always one per flower, pendulous, 45–70 mm long, 5–6 mm diam., fusiform, terete, apically strongly beaked, medium to dark brown, glabrous; *seeds* 5–6 mm long, 3.5–4 mm wide, ovate, medium brown, seta and aseta side smooth, marginally with 0.5–0.6 mm wide wing with entire to slightly lacerate margin; coma 20–25 mm long.

Chromosome number. $2n = 22$ (voucher: *Liede & Meve 2500* (MO, MSUN)).

Phenology. Collected in flower from January to October; in fruit from May to November.

Distribution. Mexico: Coahuila, Nuevo León, San Luis Potosí, Tamaulipas. U.S.A.: Texas: limestone hillsides, shale slopes, valley bottoms, in chaparral, brush or low forest; 30–2300 m.

Literature and illustrations. Henrickson (1987: 94).

Additional specimens examined. MEXICO. **Coahuila:** Cañon Loma Prieta, ca. 12 km al NE de Hipólito, 23 Oct. 1985 (fl), *Villarreal et al. 3115* (LL); Sierra de Parras, 19 Aug. 1982 (fr), *Cowan 3616*, (NY, TEX). **Nuevo León:** W of Cerralto, 29 May 1847 (fl), *Gregg s.n.* (NY); S part of Cerro Pedregoso, 1.5 km W of El Peñuelo, 18 June 1972 (fl), *Chiang et al. 7964* (LL); Chipinque, 1 July 1947 (fl), *Barkley et al. 7155* (TEX); Galeana, ca. 5 km E of La Poza toward Rio San Jose, 18 Sep. 1933 (fl), *Nesom et al. 7592* (LL); Galeana, Rancho Aguililla, 16 Sep. 1989 (fl, fr), *Hinton et al. 19732* (LL); ca. 120 km S of Laredo along Hwy. 85 to Monterrey, 10 Oct. 1982, *Henrickson 19303* (LL); near Monterrey, 2 June 1889 (fl, fr), *Pringle 2836* (HBG); Montemorelos, 8 Aug. 1989 (fl), *Liede & Conrad 2610* (MO, UBT); 3 mi. W of Montemorelos, *Gentry 6723* (ARIZ); Cerca de Monterrey, 29 June 1944 (fl), *Fernándes & Barkley 14485* (LL); Monterrey-Laredo ca. 49 km, Salinas Victoria, 3 June 1994 (fl), *Hinton et al. 24258* (LL); 12.8 mi. S of Sabinas Hidalgo on Hwy. 85, 2 July 1985 (fl, fr), *Cowan et al. 5359* (LL); Sierra Gomas, Bustamante Canyon, 12 Aug. 1988 (fl), *Patterson 6519* (TEX); San Augustine, Monterrey, 22 Apr. 1960 (fl), *Smith M124* (LL). **San Luis Potosí:** N of the Minas de San Rafael, 30 June

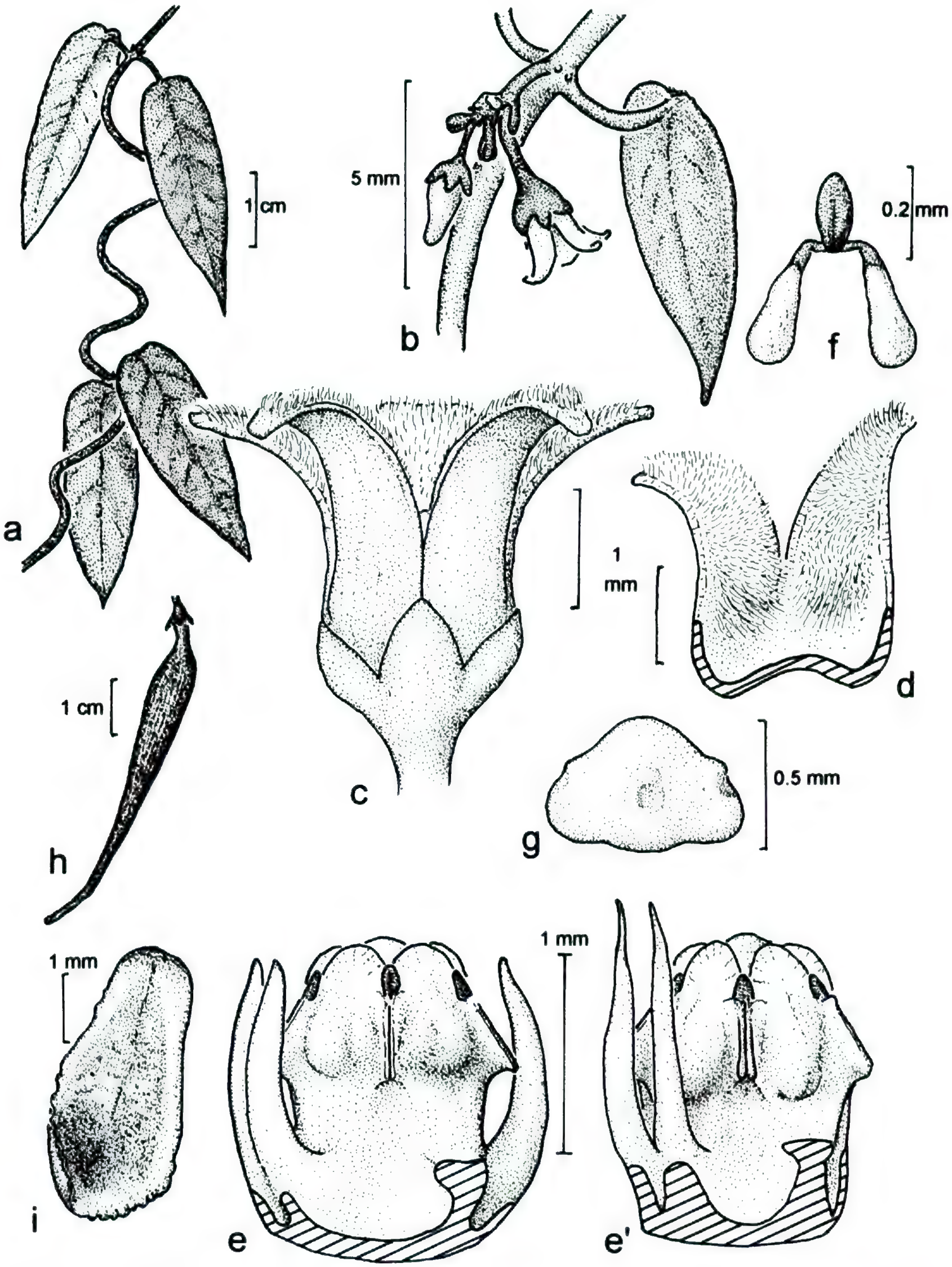


Figure 4. *Metastelma barbigerum*. a–i. *Metastelma barbigerum* var. *barbigerum*. e'. *Metastelma barbigerum* var. *liesnerianum*. —a. Habit. —b. Inflorescence. —c. Flower. —d. Corolla lobe, adaxial view. —e, e'. Corona and gynostegium. —f. Pollinarium. —g. Style-head. —h. Follicle. —i. Seed. a, b, h, i: *Correll & Johnston 19695*. e–g: *Liede & Conrad 2610*. e': *O'Neill 18659*. Drawn by J. Conrad.

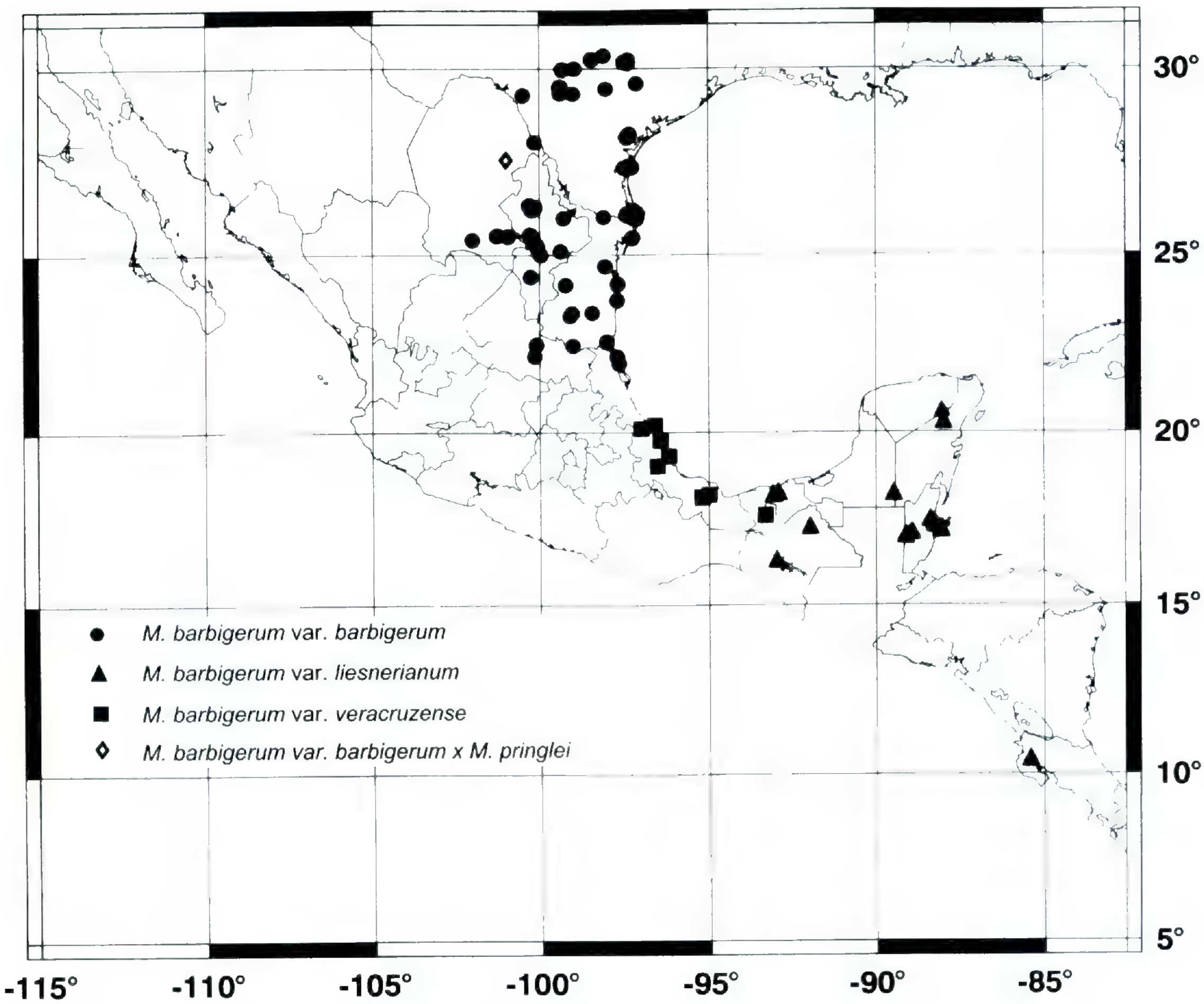


Figure 5. Distribution of *Metastelma barbigerum*.

1972 (fl), *Chiang et al. 8161D* (LL); 15.7 rd. mi. E of El Huizache jct. (at Hwy. 57) on MEX 80 to Cd. del Maiz., 24 Sep. 1978 (fl), *Henrickson & Lee 17559* (LL). **Tamaulipas:** 9 mi. NW of Chamal, just N of Ojo de Agua, 8 Feb. 1960 (fl), *Johnston 5063B* (LL); Cuatro caminos, Hidalgo, 5 June 1994 (fl), *Hinton et al. 24186* (LL); Jaumave, 24 Oct. 1978 (fl), *Calvert 117* (LL); 1 km antes de La Pesca, cerca de la Laguna Salada, 22 Sep. 1985 (fl), *Hernandez 1562* (TEX); S of Lomas del Real, 7 mi. N of main Hwy. on dirt road just N of Altamira, 27 Oct. 1959 (fl), *Johnston & Graham 4525* (LL); Punta Algodones on N end of peninsula, 12 Sep. 1981 (fl, fr), *Fryxell 3651* (NY, LL); Tampico, 15 June 1897 (fl, fr), *Pringle 6646* (HBG, NY); vicinity of Victoria, 1907 (fl), *Palmer 360* (NY); 35 km from Victoria on the road to Casas & Soto la Marina, 3 Oct. 1956 (fl), *Martinez & Luyando F-2295* (LL); 3 mi. N of Villagran on the Victoria–Linares Hwy., 12 Nov. 1959 (fr), *Johnston & Graham 4674* (LL). State not known: northern Mexico, *Wright 1676* (NY). U.S.A. **Texas:** Bandera Co., Rte. 470 betw. Tarpley and Utopia, at Hondo Creek crossing, 16 May 1984 (fl), *Ertter 5357* (NY); Bee Co., 2 mi. SW of Beeville, 17 July 1958 (fl, fr), *Correll & Johnston 19695* (NY); Brewster Co., Big Bend, Oak Springs Trail, 7 Mar. 1989 (fl), *Liede & Meve 2500* (MO, MSUN); Cameron Co., dirt road 2 mi. N of Bayview clay bank, 13 June 1967 (fl), *Crutchfield 3000* (NY); 5 mi. W of Boca Chica, 15 Mar. 1966 (fl), *Crutchfield 1125* (NY); 4 mi. NE of Port Brownsville, off F.R. 1792, 13 June 1967 (fl), *Crutchfield 2984* (NY); El Jardin, Community house No. 2, along Resaca de la Rancho Viejo, 14 Apr. 1925 (fl), *Small & Wherry 11875* (NY); Green Island, June 1922 (fl, fr), *Tharp 1185* (NY); Laguna Madre, ½–1 mi. W of Port Isabel, 26 June 1950 (fl), *Webster & Wilbur 3060* (NY); Comal Co., Old Bear Creek rd. nr. confluence of Bear Creek & Little Bear Creek, NW of New Braunfels, 2 July 1983 (fl), *Ertter 4906* (NY); Duval Co., San Diego, 1884, *Croft 62* (NY); Gillespie Co., Balanced Rock, 4 mi. N of Fredericksburgh on TX 965, 23 Aug. 1978 (fl), *Wyatt 1464* (GA); Bear Mountain, 18 June 1946 (fl), *Correll & Correll 12756* (NY); Kenedy Co., Yturria Ranch, 6 May 1940 (fl), *Lundell 8734* (NY); Kimble Co., Rocky Bluffs, *Reverchon 1558* (NY); Live Oak Co., near Mathis, 28 June 1974 (fl, fr), *McGee 134* (GA); Nueces Co., along Corpus Christi Bay, Apr. 1894 (fl), *Heller 1559* (NY); Corpus Christi, 7 May 1920 (fl), *Pennell 10220* (NY); Flour Bluff, 7 Jan. 1939 (fl), *Tharp 248* (NY); Pecos Co., Comanche Spring, New Braunfels, July 1851 (fl, fr), *Lindheimer 992* (NY); Travis Co., Austin, Eastern Texas, 1872, *Hall 521* (NY); Barton Springs Creek, 23 July 1943 (fl, fr), *Barkley 13360* (NY); Mt. Bonnel, nr. Austin, 24 June 1946 (fl, fr), *Albers et al. 46448* (S). County not known: *s. coll. (Herb. Berlandianum) 3198* (NY), *Wright s.n.* (NY).

2b. Metastelma barbigerum Scheele var. **liesnerianum** (L. O. Williams) Liede & Meve, comb. et stat. nov. Basionym: *Cynanchum liesneriana* L. O. Williams, Fieldiana, Bot. 34: 102. 1972. *Metastelma liesnerianum* (L. O. Williams) Liede, Novon 7: 42. 1997. TYPE: Costa Rica. Guanacaste: vicinty of Cañas, 11 mi. S of Liberia, 12 Dec. 1969, *K. Daubenmire 406* (holotype, F neg. 056988!). Figures 4e′, 5.

Plants ascending, 80–200 cm high; *subterranean organs* constituting a woody rootstock; *shoots* perennial, basally slightly woody with yellowish bark, glabrous or sparsely covered along a single line with recurved trichomes, 200–250 μm long; internodes 2.5–4 cm long, to 1 mm diam. *Leaves* with petioles 2–5 mm long, with 0 to 2 colleters at blade base; blades 20–35 × 4–15 mm, ovate to elliptic, basally obtuse to rounded, apically acute to acuminate, adaxially glabrous or with isolated recurved trichomes, 200–300 μm long mainly on veins and margins, abaxially glabrous. *Inflorescences* always one per node, 2- to 5-flowered, 1 to 5 flowers open synchronously, sciadioidal, bostrychoid, sessile to pedunculate with to 3 mm long peduncles, glabrous or sparsely covered along a single line with recurved trichomes, 150–200 μm long; rachis 1–2 mm long, straight; *floral bracts* 4–6 × 2–3 mm at the base, deltoid to ovate, glabrous; *pedicels* 2–3 mm long, glabrous. *Floral buds* 2–2.5 mm long, 1–1.3 mm diam., ovoid to conical; *calyx* basally fused, rotate to campanulate, abaxially with a few trichomes on the calyx tube (characteristic for this variety); calyx lobes 0.7–1 × 0.2–0.4 mm, ovate, apically obtuse to acute; *corolla* 2–3 mm long, abaxially white, glabrous, adaxially white, with verrucose trichomes, 100–150 μm long, on the apical and on the lateral parts of the lobes, and smooth, downward-directed trichomes, 250–300 μm long, on the central parts of the lobes; lobes 0.8–1 mm wide, suberect, apically acute, recurved, with straight to slightly revolute margins; *gynostegial corona* 1–1.2 mm long, equaling to slightly longer than the gynostegium; lobes erect, attached near the base of the stipe, laminar, ovate, with entire margins. *Gynostegium* 0.4–0.6 mm high, 0.8–1 mm diam., on a stipe 0.3–0.4 mm long; *anthers* broader than high, trapezoidal, abaxially planar to convex; anther wings 300–400 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther to slightly centrifugal; connective appendages 300–400 μm long, 200–300 μm wide, ovate to triangular, equaling the stamen in width, slightly inflexed; *pollinarium* with corpusculum 150–200 μm long, between 1.5 times and twice as long as broad, ovoid; caudicles 60–80 μm long, cylindrical to flattened, s-shaped, concave-convex; pollinia apically attached to the caudicles, 150–200 μm long, 80–100 μm wide, clavate; *stylehead* white, ca. 0.5 mm diam., ca. 0.3 mm high, upper part ca. 0.15 mm high, equaling to longer than the lower part, flat to depressed-conical. *Follicles* always one per flower, pendulous, 35–40 mm long, 2 mm diam., terete, apically strongly beaked, dark brown when dried, glabrous.

Phenology. Collected in flower from January to August and in October; in fruit in January.

Distribution. Belize; Costa Rica: Guanacaste; Guatemala: Péten; Mexico: Campeche, Chiapas, Tabasco, Yucatán; close to rivers, on disturbed slopes; low altitudes, to 200 m.

Literature and illustrations. Williams (1972: 103, fig. 1A–C).

Additional specimens examined. BELIZE. Hector Creek, Sibun River, 6 Mar. 1935 (fl), *Gentle 1508* (NY); Pine Ridge, 12 km N of Belize, 22 Aug. 1936 (fl), *O'Neill 8659* (WIS); Mile 5 ¾ Northern Hwy., 7 June 1974, *Dwyer 12774* (NY); Vaca, 25 Apr. 1938 (fl), *Gentle 2517* (NY); betw. Belmopan & San Ignacio, 13 Feb. 1995 (fl), *Liede 3242* (UBT). GUATEMALA. **Petén:** Dos Lagunas, El Cedro, 4 May 1969 (fl, fr), *Contreras 8466* (NY, TEX); Tikal Nat. Park, Bajo de Santa Fe, 29 Jan. 1960, *Contreras 532* (LL). MEXICO. **Campeche:** 2 Oct. 1847 (fl), *Edwards s.n.* (NY); 1 km al Sureste de Conhuas dirección Calakmul, 150 m, 4 Aug. 1995 (fl), *Gutiérrez 4632* (TEX). **Chiapas:** Aguacate Palenque, 16 July 1939 (fl), *Matuda 3765* (LL, NY); 17 km N of Tuxtla Gutiérrez along road to El Sumidero, 30 Oct. 1965 (fl), *Breedlove 14010* (TEX). **Tabasco:** Jalapita, 8 July 1962 (fl, fr), *Sauer & Gade 3137b* (WIS); Laguna Mecoacan, 16 May 1963 (fl), *Barlow 28/17* (WIS). **Yucatán:** Izamal, 1895, *Gaumer 539* (NY, UPS, WIS).

2c. Metastelma barbigerum Scheele var. **veracruzense** Liede & Meve, var. nov. TYPE: Mexico. Veracruz: 48 km SE of Nautla, 30 Dec. 1972, *J. Taylor & C. Taylor 12532* (holotype, NY!). Figure 5.

Haec varietas varietati *liesneriano* similis, sed differt pedicellis calycibusque pubescentibus.

Plants ascending, 200 cm high; *shoots* perennial, covered along a single, but occasionally a broad line of recurved to flexuous trichomes, 300–400 μm long. *Leaves* with petioles 2–7 mm long, with 0 to 2 colleters at blade base; blades 10–45 × 6–15 mm, basally obtuse to rounded, apically acuminate to acute, adaxially glabrous or with isolated recurved trichomes, 250–300 μm long, mainly on veins and margins; abaxially sparsely covered only on the midrib with recurved trichomes, ca. 300 μm

long. *Inflorescences* always one per node, 2- to 7-flowered, 2 to 7 flowers open synchronously, sciadioidal; *peduncles* 1–4 mm long, sparsely to densely covered along a single line or over the entire surface with flexuous trichomes, 150–200 μm long; *floral bracts* 0.4–0.8 × 0.2–0.3 mm at the base, triangular to ovate, sparsely with trichomes on the surface; *pedicels* 2–4 mm long, densely covered over the entire surface with flexuous trichomes, ca. 200 μm long. *Floral buds* ca. 2 mm long, ca. 1 mm diam., conical, with imbricate aestivation; *calyx* basally fused, rotate to campanulate, ciliate or abaxially with trichomes (mainly on the tube); calyx lobes 1–1.2 × 0.5–0.6 mm, ovate, apically acute; *corolla* rotate to campanulate, 2–3 mm long, abaxially white, glabrous, adaxially white, adaxially with verrucose trichomes, 100–150 μm long, on the apical and on the lateral parts of the lobes and downward-directed smooth trichomes, 250–300 μm long, on the central parts of the lobes; lobes fused to ca. ⅓ of total corolla length, 0.6–0.8 mm wide, erect to patent, ovate, apically acute; *gynostegial corona* 0.8–1 mm long, equaling to longer than the gynostegium; lobes erect, attached along the stipe, laminar, very narrowly ovate. *Gynostegium* ca. 0.6 mm high, ca. 1 mm diam., on a stipe 0.3–0.5 mm long; *anthers* broader than high, trapezoidal, abaxially planar; anther wings 300 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther; connective appendages 300–350 μm long, 250–300 μm wide, ovate, narrower than the stamen, slightly inflexed; *pollinarium* with corpusculum 150–200 μm long, between 1.5 times and twice as long as broad, elliptic; caudicles 50–60 μm long, flattened, s-shaped, concave-convex; pollinia subapically attached to the caudicles, ca. 200 μm long, ca. 100 μm wide, ovoid; *style-head* white, ca. 0.7 mm diam., ca. 0.5 mm high, upper part ca. 0.25 mm high, equaling the lower part, flat to depressed-conical. *Follicles* always one per flower, 30–40 mm long, 4–6 mm diam., obclavate, straight, apically strongly beaked, green-brown, glabrous; *seeds* 5–6 mm long, 2.5–3 mm wide, ovate, medium to dark brown, seta side tuberculate, papillose with regularly arranged papillae, aseta side vaguely tuberculate, marginally with 0.2–0.3 mm wide wing with denticulate margin; coma 25–30 mm long.

Phenology. Collected in flower from August to December; in fruit in December.

Distribution. Mexico: Tabasco, Veracruz; sand dunes and savanna borders; 0–50 m.

Cowan & Magaña 3270 (NY) from Huimanguillo, Tabasco, is not entirely glabrous like variety *liesnerianum*, but not as densely indumented as the other *Metastelma barbigerum* var. *veracruzense* specimens.

There is a second NY specimen of *Purpus 2094*, which is referred to *M. schlechtendalii* var. *schlechtendalii*.

The *Metastelma barbigerum* complex is characterized by mostly glabrous stems (but with a single line of trichomes in var. *veracuzense*), conically shaped gynostegia with obliquely protruding anther wings (guide rails) and corona lobes that hardly exceed the anthers (Figs. 1a, c, e, f; compare also Henrickson, 1987). The two southern varieties differ in the attachment of the corona lobes, which is not as distinctly hook-shaped as in the typical variety. The distribution of this complex is confined to the eastern landmasses surrounding the Gulf of Mexico.

Paratypes. MEXICO. **Tabasco:** Huimanguillo, km 39.7 de la desviación de Humanguillo hacia Fco. Rueda, 10 Oct. 1980 (fl), *Cowan & Magaña 3270* (NY). **Veracruz:** Rte. 180, 130 km NW Catamaca, 16 Sep. 1970 (fl), *Burch 2984* (NY); alrededores de la planta Laguna Verde, 11 Nov. 1975 (fl), *Dorantes 5270* (NY); about 4.5 mi. W of Palmilla along Hwy. through Huatusco, 10 Aug. 1971 (fl), *Stevens 1409* (NY); Tecolutla, 20 Dec. 1963 (fl, fr), *Cavender s.n.* (WIS); Zacuapan and vicinity, Nov. 1906 (fl), *Purpus 2094* (HBG, NY).

3. Metastelma californicum Benth., in Hinds, R. B., Bot. Voy. Sulphur: 33, pl. 18. 1844. *Cynanchum californicum* (Benth.) Moran, in Levin & Moran, Vascular Fl. Isla Socorro Mexico (Mem. San Diego Soc. Nat. Hist. 16): 26. 1989. TYPE: Mexico. Baja California: Magdalena Bay, *G. Bentham s.n.* (holotype, K!). Figures 6a–f, 8.

3a. Metastelma californicum Benth. subsp. **californicum**

Plants ascending, 50–150 cm high; *shoots* annual, basally woody, with gray-brown bark, glabrous or isolatedly glabrescent along a single line with flexuous trichomes, 200–300 μm long; internodes 2–4 cm long, 0.5–0.8 mm diam. *Leaves* with petioles 3–6 mm long, with 2 colleters at blade base; blades 10–20(–25) × 4–10(–14) mm, ovate to elliptic, basally rounded, apically acute to acuminate, adaxially sparsely covered on the midrib and the margins with flexuous trichomes, 200–300 μm long, abaxially glabrous. *Inflorescences* always one per node, 2- to 6-flowered, 2 to 3 flowers open synchronously, sciadioidal, subsessile; *floral bracts* 0.5–0.6 × 0.2–0.3 mm at the base, triangular, gla-

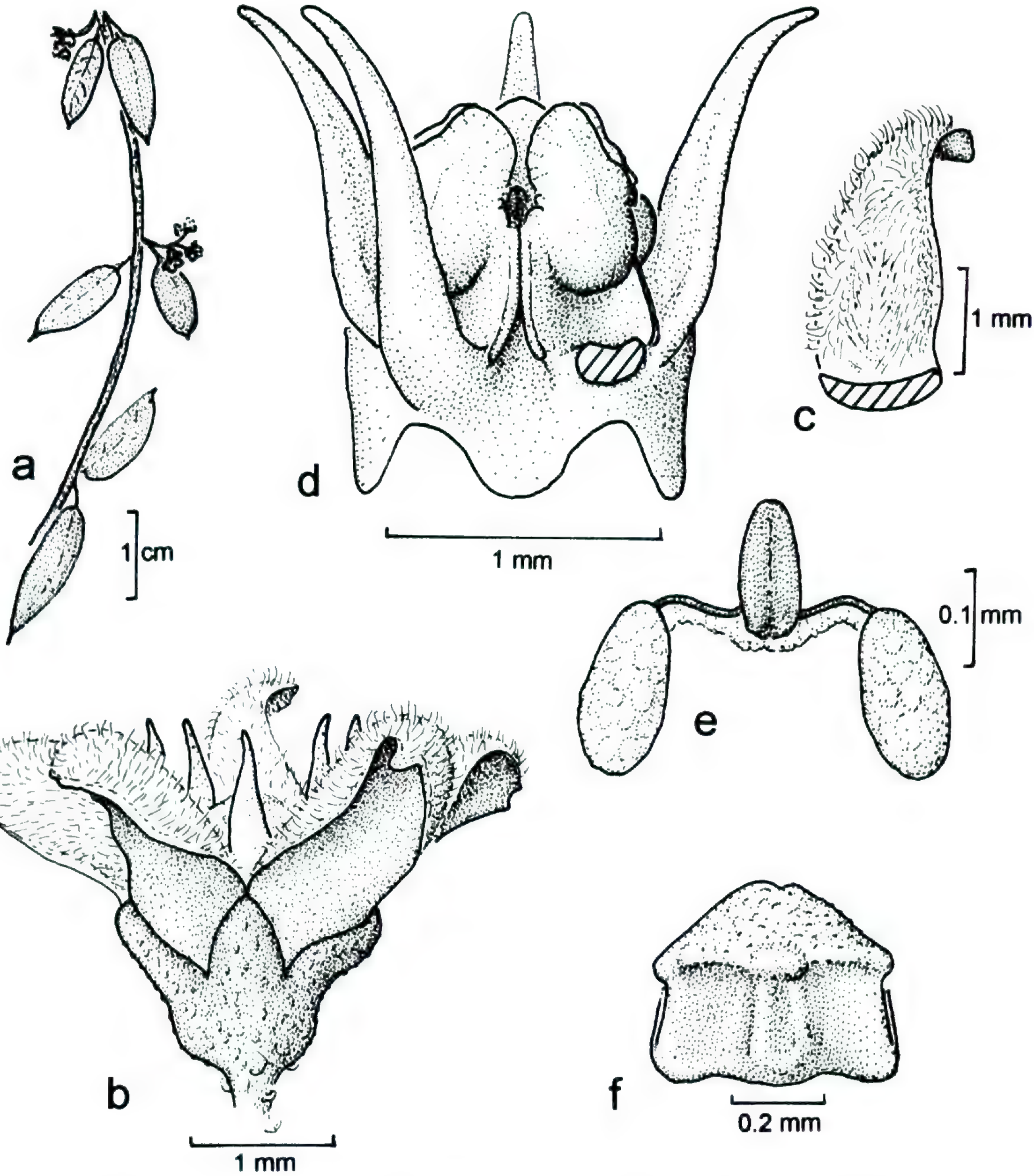


Figure 6. *Metastelma californicum* subsp. *californicum*. —a. Shoot with inflorescences. —b. Flower. —c. Corolla lobe, adaxial view. —d. Gynostegium and corona. —e. Pollinarium. —f. Style-head. a: *Brandegee s.n.* b–f: *Liede & Conrad 2955*. Drawn by J. Conrad.

brous; *pedicels* 3–4 mm long, glabrous or with a few isolated trichomes. *Floral buds* ca. 2 mm long, ca. 1.5 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially glandular, glabrous; calyx lobes 1–1.2 × 0.4–0.6 mm, ovate, apically acute; *corolla* campanulate to rotate, 2.5–3.5 mm long, abaxially white, purplish along the main nerves, glabrous, adaxially white, with verrucose trichomes, 200–250 μm long, on the apical and on the lateral parts of the lobes and with smooth, downward-directed trichomes, 180–220 μm long, on the central parts of the lobes; lobes basally fused, 1–1.2 mm wide, patent to erect, ovate, apically acute to obtuse; *gynostegial corona* 1.3–1.5 mm long, slightly longer than the gynostegium; lobes erect, attached directly underneath the anthers, laminar, lanceolate. *Gynostegium* ca. 1 mm high, ca. 0.9 mm diam., sessile; *anthers* higher than broad, rectangular, abaxially gibbous; anther wings ca. 500 μm long, extending along the entire length of the anther or beyond, anther wings of adjacent anthers divergent toward the base, in the same plane as the anther; connec-

tive appendages 300–400 μm long, ca. 300 μm wide, ovate, equaling the stamen in width, slightly inflexed; *pollinarium* with corpusculum 140–150 μm long, between 1.5 times and twice as long as broad, ovoid; caudicles 60–70 μm long, cylindrical to flattened, straight, ascending, slightly thickened at the insertion of the pollinium; pollinia subapically attached to the caudicles, 180–220 μm long, 80–90 μm wide, ovate in cross section, ovoid; *stylehead* white, ca. 0.5 mm diam., ca. 0.4 mm high, upper part ca. 0.2 mm high, equaling the lower part, conical. *Follicles* always one per flower, 50–60 mm long, 4–6 mm diam., fusiform, terete, apically strongly beaked, wingless, dark brown, glabrous; *seeds* 5–6.5 mm long, 2.5–3 mm wide, ovate, dark brown, seta and aseta side tuberculate, marginally wingless, entire; coma 10–20 mm long.

Phenology. Collected in flower from October to April and in July and August; in fruit in December, February, March, and October.

Distribution. Mexico: Baja California, Sinaloa, Sonora, Revillagigedo Islands; on rocky slopes and in sandy washes, very dry desert vegetation; 0–640 m.

Literature and illustrations. Bentham (1844: pl. 18).

Additional specimens examined. MEXICO. **Baja California:** 3.2 mi. NW of Arroyo Palmarito via Hwy. 1, 21 July 1990 (fl, fr), *Burgess & Van Devender 7661* (ARIZ); E of Arroyo Seco, 21 Mar. 1935 (fl, fr), *Shreve 7197* (ARIZ); Catavina, 76 mi. S of El Rosario on Mex. Hwy. 1, 13 Dec. 1977, *Nixon & Cowan 831* (LL); 2 mi. NW of Catavina, 29 Apr. 1980 (fl), *Davis & Lightowlers 66297* (B); Cerro Tordillo & vicinity, Systema de la Sierra Viscaino, 12 Mar. 1947 (fl), *Gentry 7438* (ARIZ); Escondito Creek, 7 Mar. 1934 (fl, fr), *Shreve 6468*, (ARIZ); Escondido Canyon betw. Punta Prieta & ocean, 7 Mar. 1934 (fl), *Ferris 8589* (NY); 8 mi. N of Mt. Mesquital Grande, 9 Feb. 1935 (fl), *Haynes & Stewart s.n.* (NY); 6 mi. S of Laguna Chapala Seca, 17 Oct. 1959 (fl), *Wiggins 15048* (ARIZ); Picacho de Santa Clara, Nov. 1947 (fl), *Gentry 7716* (ARIZ); Playa San Pedrito, Los Cerritos, al SW de Todos Santos, 13 Oct. 1985 (fl, fr), *Tenorio et al. 10441* (MO); 10–20 km N of Puerto Santa Catarina on rd. to Rancho Santa Catarina, 1 Mar. 1985 (fl), *Breedlove 62261* (NY); 20–30 mi. S of Punta Canoas along tract to Punta Cono, 27 Feb. 1986 (fl), *Breedlove 62528* (LL); 12.1 mi. (by rd.) N of Punta Prieta, 17 Oct. 1967 (fl), *Hastings & Turner 67-64* (ARIZ); just 2.5 mi. S of Punta Prieta, 17 Oct. 1959 (fl, fr), *Wiggins 15085* (ARIZ); just S of Rosarito, 14 Mar. 1979 (fl, fr), *McLaughlin & Bowers 2119* (ARIZ); Todos Santos, ca. 8 km on track to Sierra Laguna, 20 Jan. 1992 (fl, fr), *Liede & Conrad 2955* (ULM); Todos Santos, Jan. 1890 (fl), *Brandegee s.n.* (NY); Turtle Inlet, Magdalena Bay, 10 Aug. 1932 (fl), *Howell 10639* (NY). **Sinaloa:** Isla Tachechilte, 3–10 m, 20 Jan. 1945, *Gentry 7136* (ARIZ, NY). **Sonora:** Isla San Pedro Nolasco, E side of island, Nov. 26, 1963, *Felger 9635* (ARIZ, LL); Las Bocas on the coast of the Gulf of California, 1 Feb. 1992 (fl, fr), *Van Devender et al. 92-121* (ARIZ); Loma Chomajabires, 1.8 mi. N of Huatabampito, 23 Dec. 1995, *Fishbein & McMahon 2750* (ARIZ), *2769* (ARIZ). **Revillagigedo Islands:** Socorro Island, 24 May 1903, *Barkelew 217* (ARIZ, NY).

3b. Metastelma californicum Benth. subsp. **lanceolatum** (Schltr.) Liede & Meve, comb. et stat. nov. Basionym: *Metastelma lanceolatum* Schltr., Bull. Herb. Boissier 6: 840. 1906. TYPE: Mexico, San Luis Potosí: San José Pass, 12 July 1890, *C. G. Pringle 3138* (neotype, designated here, M!; isotypes, HBG!, NY!). Figures 7a–g, 8.

Ditassa mexicana Brandegee, Univ. Calif. Publ. Bot. 10: 414. 1924. Syn. nov. TYPE: Mexico, Chiapas: Hacienda Montserrate, Sep. 1923, *C. A. Purpus 9167* (holotype, UC 220412 not seen; isotypes, GH!, NY!).

Plants ascending, to 250 cm high; *shoots* perennial, basally woody, with brownish bark, sparsely covered along a single line with recurved trichomes, 150–300 μm long; internodes 1.7–7 cm long, to 1 mm diam. *Leaves* with petioles 3–5 mm long, with 2 colleters at blade base; blades 15–35 × 3–16 mm, ovate to oblong, basally rounded, apically acute to acuminate, adaxially sparsely covered only on the midrib and the margins or over the entire surface (*Roe & Roe 1885*) with erect to recurved trichomes, 200–350 μm long, abaxially glabrous (occasionally with a few trichomes on the midrib). *Inflorescences* always one per node, 4- to 7-flowered, 1 to 7 flowers open synchronously, sciadioidal, subsessile; *floral bracts* 0.5–0.6 × 0.3–0.4 mm at the base, triangular, glabrous or ciliate; *pedicels* 2–3 mm long, glabrous or sparsely covered along a single line with flexuous trichomes, ca. 200 μm long (*Roe & Roe 1885*). *Floral buds* 2–2.5 mm long, 1.3–1.5 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially glabrous or with trichomes on the tube (*Roe & Roe 1885*); calyx lobes 0.8–1 × 0.4–0.6 mm, ovate, apically acute; *corolla* rotate to cyathiform, 2.5–3 mm long, abaxially greenish white, adaxially white or cream, with verrucose trichomes, 120–180 μm long, on the apical and on the lateral parts of the lobes and smooth trichomes, 180–200 μm long, on the central parts of the lobes; lobes basally fused, 1–1.2 mm wide, patent, ovate, apically acute to obtuse; *gynostegial corona* 0.8–1.2 mm long, equaling to longer than the gynostegium; lobes erect, attached directly underneath the anthers, laminar, ovate, apically acute to longly acuminate. *Gynostegium* 1–1.3 mm high, 1.2–1.5 mm diam., sessile; *anthers* about as high as broad, rectangular, abaxially gibbous; anther wings 500–600 μm long, extending along the entire length of the anther, anther wings of adjacent anthers par-

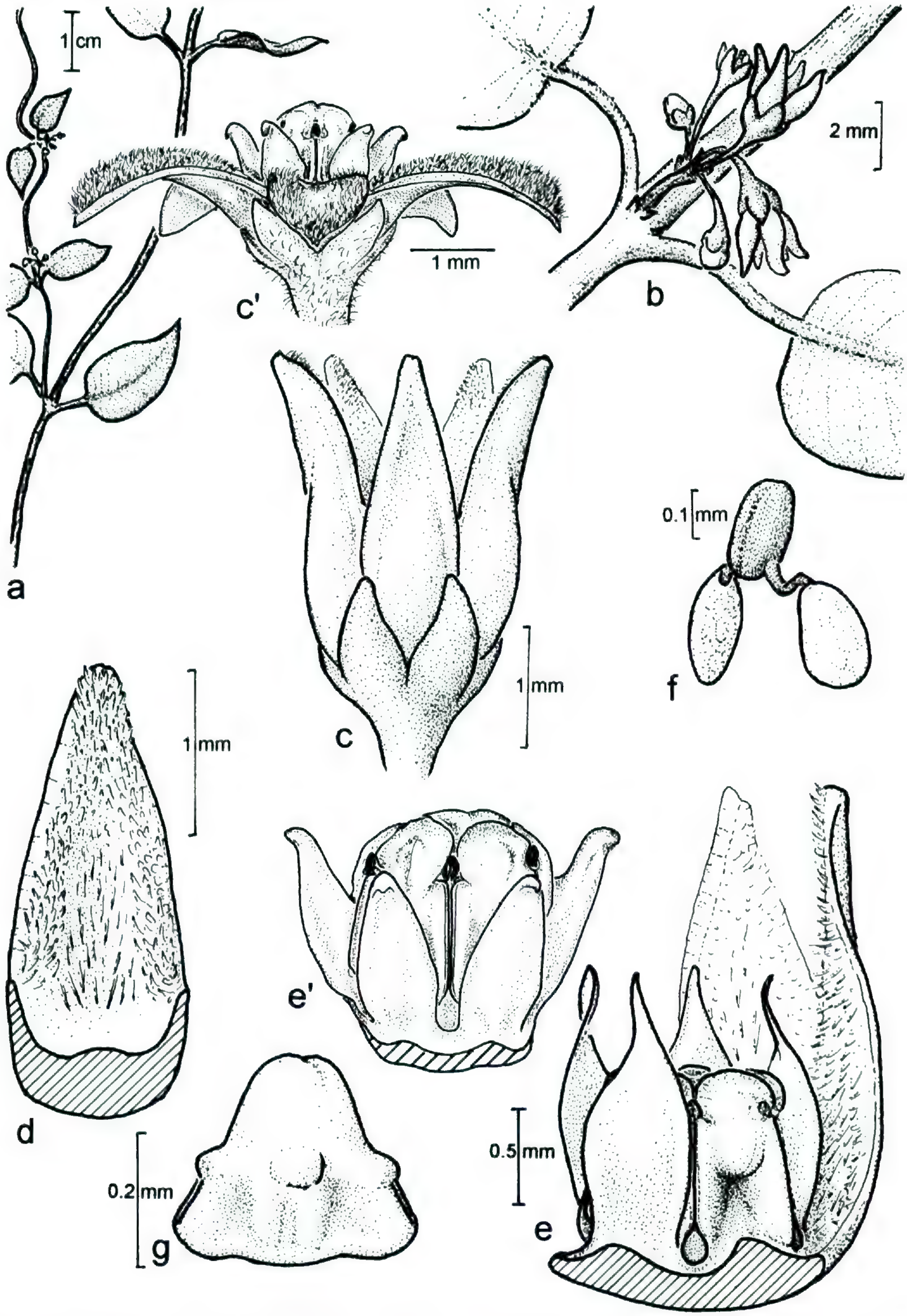


Figure 7. *Metastelma californicum* subsp. *lanceolatum*. —a. Habit. —b. Shoot with inflorescence. —c, c′. Flower. —d. Corolla lobe, adaxial view. —e, e′. Corona and gynostegium. —f. Pollinarium. —g. Style-head. a–g: *Purpus 9167*, drawn by J. Conrad. c′, e′. *Roe & Roe 1885*, executed by U. Meve after sketch by J. Conrad.

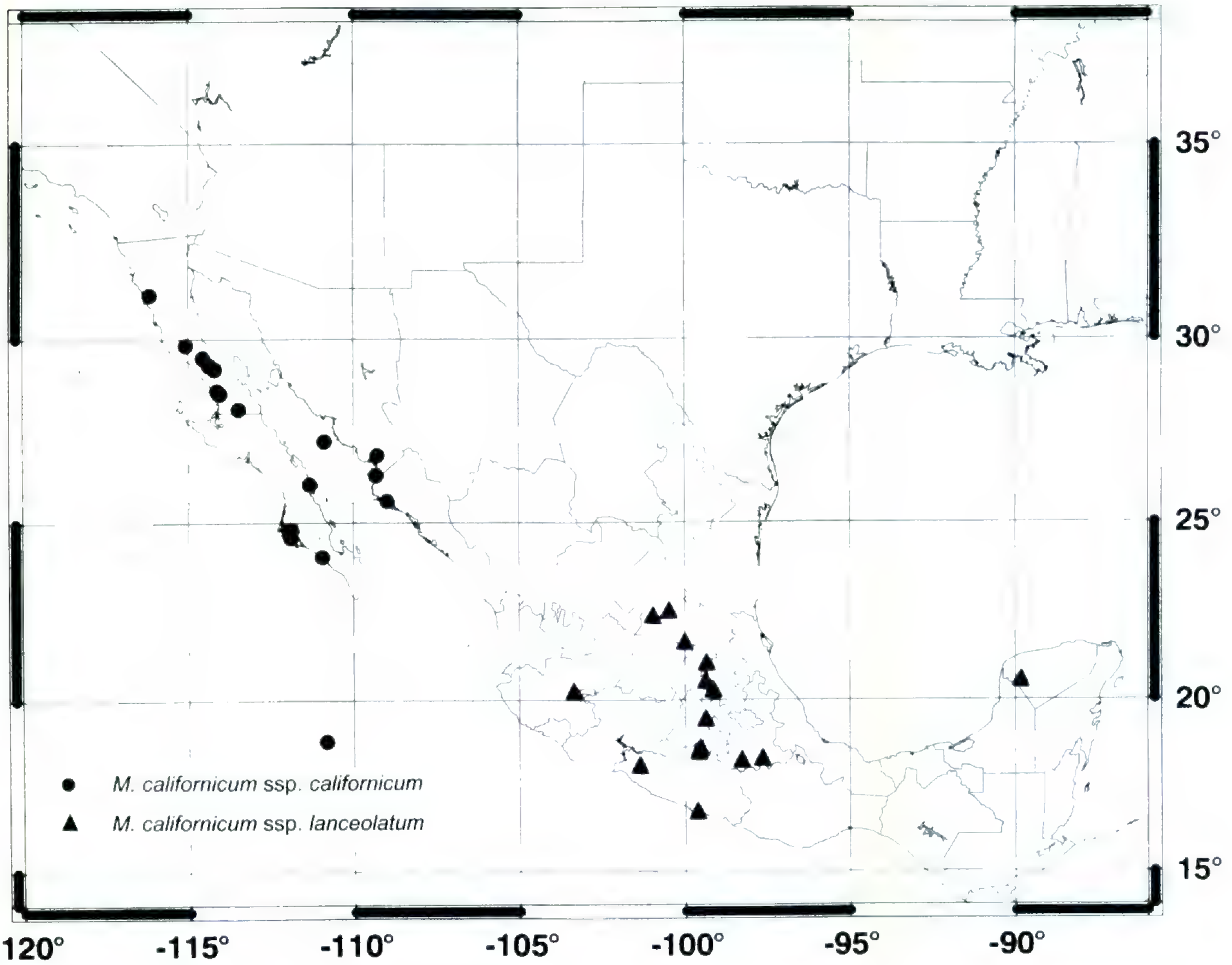


Figure 8. Distribution of *Metastelma californicum*.

allel to each other, in the same plane as the anther; connective appendages ca. 400 µm long, ca. 400 µm wide, ovate, equaling the stamen in width, slightly inflexed; *pollinarium* with corpusculum 160–180 µm long, between 1.5 times and twice as long as broad, ovoid; caudicles 60–80 µm long, cylindrical to flattened, ± straight, horizontal to convexly recurved; pollinia subapically attached to the caudicles, 280–300 µm long, ca. 120 µm wide, ovate in cross section, ovoid; *style-head* white, 0.7–0.9 mm diam., 0.4–0.6 mm high, upper part 0.3–0.4 mm high, equaling to longer than the lower part, conical. *Follicles* always one per flower, 35–45 mm long, 4–6 mm diam., obclavate, terete, apically strongly beaked, dark brown, longitudinally grooved; *seeds* ca. 5 mm long, ca. 3 mm wide, ovate, medium brown, seta and aseta side smooth, marginally with 2 mm wide wing with denticulate margin; coma 15–25 mm long.

Phenology. Collected in flower in February, May, and from July to October; in fruit in February, August, and September.

Distribution. Mexico: Chiapas, Guerrero, Hidalgo, Jalisco, México Distrito Féderal, Morelos, Oaxaca, Puebla, San Luis Potosí, Yucatán; on limestone slopes in scrub vegetation and deciduous tropical forest; 1000–2200 m.

For *Metastelma lanceolatum*, Schlechter (1906) cited the type as follows: "Mexico. Oaxaca: Distr. Tlacolula, prope Zoquitlan, flor. Jun, *C. Seler & E. Seler 72.*" However, the first set of collections of *Seler & Seler* was housed in B (Vegter, 1986), and the type of *M. lanceolatum* was probably destroyed during the second World War. It is not duplicated in any of the herbaria consulted for this study. The specimen selected as neotype (*Pringle 3138*, NY) bears the annotation "*Metastelma lanceolatum* Schltr." in Schlechter's own handwriting.

The protologue of *Ditassa mexicana* states explicitly "corona duplici," which is the generic character of *Ditassa*. No other "*Ditassa*" specimen except for the type of *Ditassa mexicana* was ever collected in Central America. However, none of the flowers examined had a double corona. This specimen exhibits the characters of *Metastelma californicum* subsp. *lanceolatum*, so that *Ditassa* remains a genus restricted to South America.

Metastelma californicum is easily distinguished

from all other Central American *Metastelma* species by a stout, sessile gynostegium with anther wings (guide rails) as long as the gynostegium. The corona is spreading and hardly exceeds the gynostegium. Morphological differences between the two subspecies of *M. californicum* mainly concern the shape of the corona lobes. As separation is both geographical and ecological, with the typical subspecies occurring in very dry desert vegetation below 640 m, and *M. californicum* subsp. *lanceolatum* in scrub vegetation and deciduous tropical forest between 1000 and 2200 m, subspecific rank, as in the parallel case of *M. arizonicum*, is warranted.

Additional specimens examined. MEXICO. **Distrito Federal:** 9 km N of Ixtan de la Sal, at km 138 on Hwy. 55, 9 Sep. 1965 (fl), *Roe & Roe 1885* (NY, WIS); Volcán, 2 Feb. 1935 (fl, fr), *Hinton et al. 7310* (NY). **Guerrero:** Acapulco, Copacabana, 15 Aug. 1970 (fl), *Boege 1438* (FR); La Posa del Lago Tres Palos, Copacabana, 19 Sep. 1969 (fl), *Boege 862* (FR). **Hidalgo:** Barranca de Tolantongo, 8 Aug. 1991 (fl), *Fernández 4731* (LL, NY); slopes of Barranca de Tolimán, 8 Aug. 1948, *Moore & Wood* 4409 (LL); El Capulin, near km 134 on highway betw. Actopan & Ixmiquilpan, 4 Aug. 1948 (fl, fr), *Moore & Wood 4259* (LL); Jacala, 2 July 1939 (fl), *Chase 7418* (ARIZ, NY). **Jalisco:** Ladera noroeste del Cerro de la Lima, 30 July 1995 (fl), *Machuca 7400* (LL). **Morelos:** near Cuernavaca, 14 Oct. 1909 (fl), *Pringle 10838* (ARIZ, TEX). **Oaxaca:** Chinantla, *Galeotti 1571* (NY). **Puebla:** 11 km al SE de San Juan Ixcaquixtla, 5 July 1986 (fl), *Salinas & Tenorio 3294* (ARIZ, LL). **San Luis Potosí:** above San Pedro, 29 July 1934 (fl), *Pennell 17729* (NY); Bocas, 5 Sep. 1939 (fl, fr), *Shreve 9312* (ARIZ); Hwy. Valles to Rioverde at km 81-½, 25 May 1981 (fl), *Fryxell & Anderson 3617* (NY). **Yucatán:** above Calcehtok, 21 Feb. 1982 (fl), *White & Mott 74* (NY).

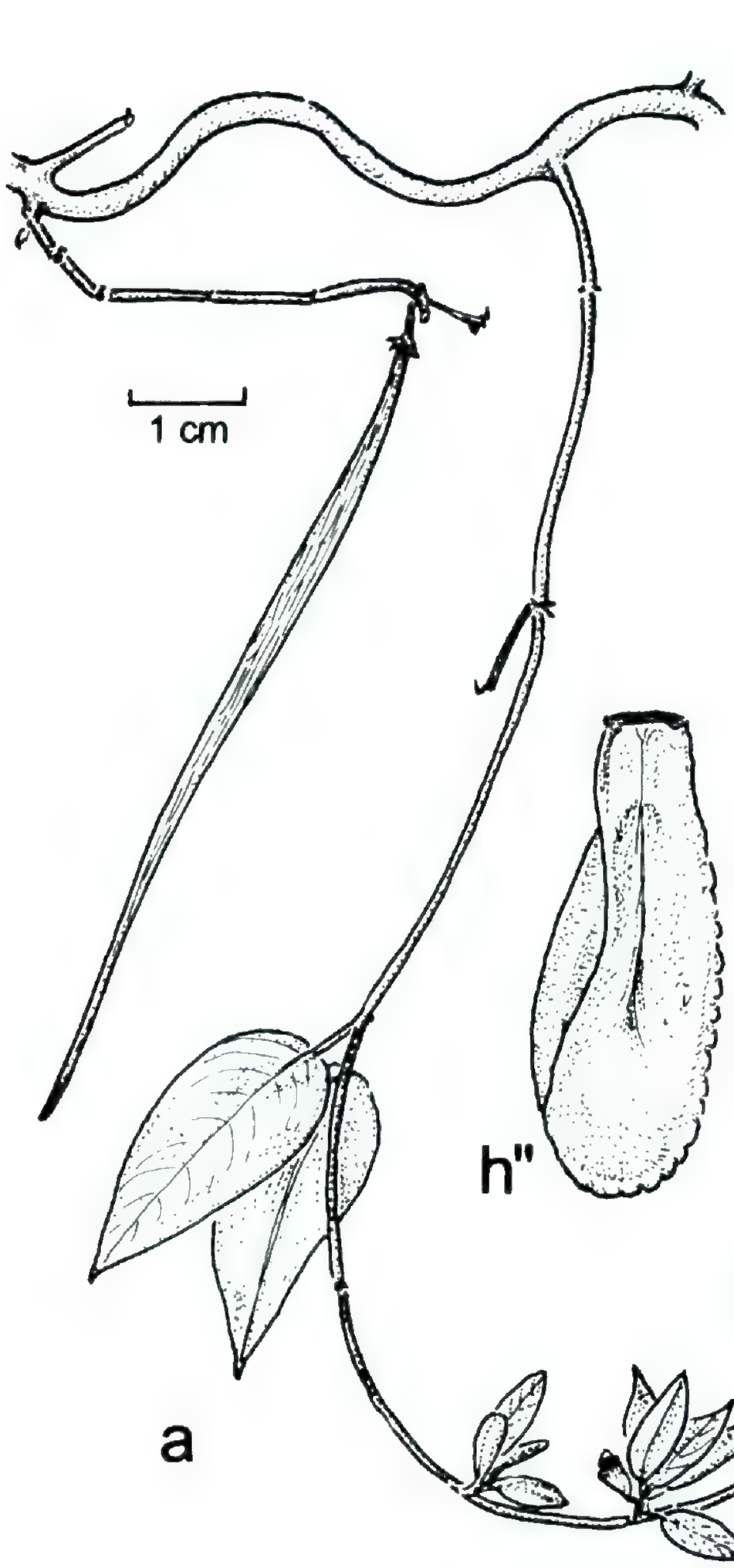
4. Metastelma cuneatum Brandegee, Zoe 5: 216. 1905. TYPE: Mexico. Sinaloa: Yerba Buena, vicinity of Culiacan, 10 Sep. 1904, *T. S. Brandegee s.n.* (holotype, UC not seen; isotypes, GH!, US!). Figures 9a–h, 10.

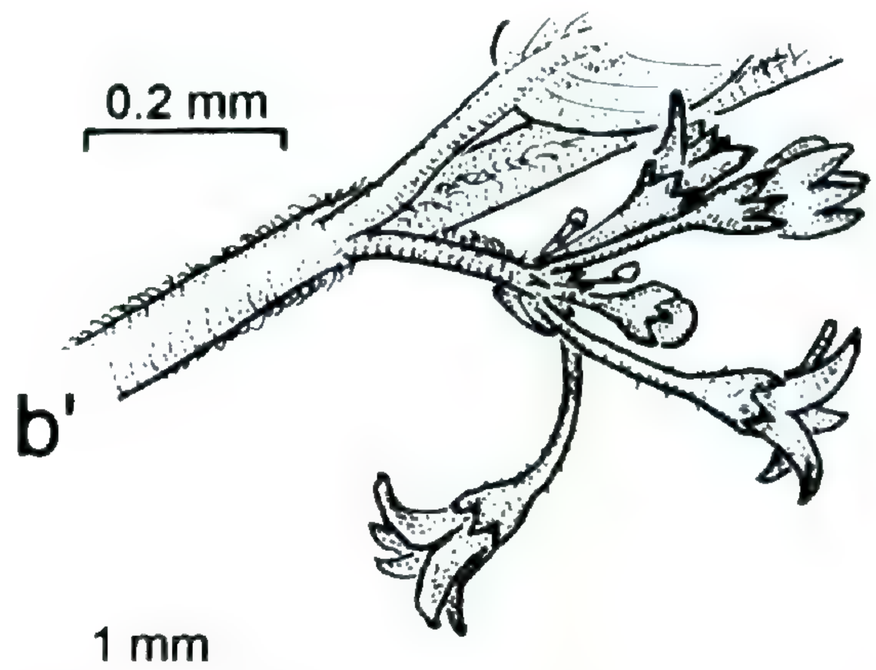
Plants ascending, 200–300 cm high; *shoots* perennial, basally woody with grayish brown bark, sparsely to densely covered along a single line with erect to recurved trichomes, 300–400 μm long; internodes 1.8–3 cm long, ca. 1 mm diam. *Leaves* with petioles 2–4 mm long, with 2 colleters at blade base; blades 15–20 × 3–7 mm, ovate to oblong, basally obtuse, apically obtuse or acuminate, adaxially sparsely covered, only on the midrib with appressed to recurved trichomes, 200–300 μm long, abaxially glabrous. *Inflorescences* one, occasionally two per node, 3- to 8-flowered, 2 to 6 flowers open synchronously, sciadioidal; *peduncles* 0.5–3 mm long, sparsely covered along a single line with erect trichomes, 150–200 μm long; *floral bracts* 0.2–0.5 × 0.2–0.3 mm at the base, triangular, elongated-triangular or ovate, with scattered trichomes on the surface; *pedicels* 3–4 mm long, glabrous, isolatedly to sparsely covered along a single line with flexuous trichomes, 200–250 μm long. *Floral buds* 1–1.3 mm long, 0.8–1 mm diam.; *calyx* fused for ca. ⅓ of its length, campanulate, abaxially glandular; calyx lobes 0.6–0.8 × 0.2–0.3 mm, ovate, apically acute; *corolla* rotate, 1.5–2 mm long, abaxially yellowish green, glabrous, adaxially white, with verrucose trichomes, 50–100 μm long, on the apical and on the lateral parts of the lobes; and with a few slightly longer, retrorse and smooth trichomes on the central parts of the lobes; lobes basally fused, 0.3–0.5 mm wide, erect to incurved, ovate, apically acute; *gynostegial corona* 0.5–0.7 mm long, equaling to shorter than the gynostegium; lobes erect to inflexed, attached directly underneath the anthers, laminar, ovate to triangular. *Gynostegium* 0.5–0.6 mm high, 0.7–0.8 mm diam., sessile to on a column ca. 0.3 mm long; *anthers* about as high as broad, rectangular, abaxially convex; anther wings 400–500 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, basally widened, in the same plane as the anther, basally forming a distinct "mouth" with the basal lateral margin of the anther; connective appendages ca. 500 μm long, ca. 400 μm wide, ovate, equaling the stamen in width, strongly inflexed; *pollinarium* with corpusculum ca. 120 μm long, more than twice as long as broad, slenderly oblongoid; caudicles ca. 100 μm long, cylindrical, s-shaped, convex-concave, thickened at the insertion of the pollinium; pollinia subapically attached to the caudicles, ca. 150 μm long, ca. 50 μm wide, ovate in cross section, reniform; *stylehead* ca. 0.7 mm diam., 0.35 mm high, forming distinct noses at upper ends of corpusculi, upper part ca. 0.15 mm high, shorter than the lower part, depressed-conical. *Follicles* always one per flower, 60–80 mm long, 4–5 mm diam., very slender fusiform, terete, apically shortly beaked, grayish brown, glabrous; *seeds* 6–7 mm long, 3–3.5 mm wide, pyriform, medium brown, seta side vaguely tuberculate, aseta side smooth, marginally with 0.2–0.3 mm wide wing with denticulate margin; coma 25–30 mm long.

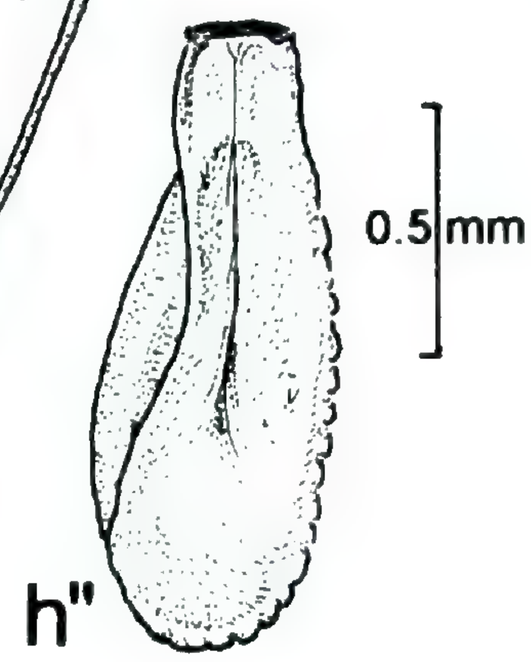
Phenology. Collected in flower in September and from November to January; in fruit in January.

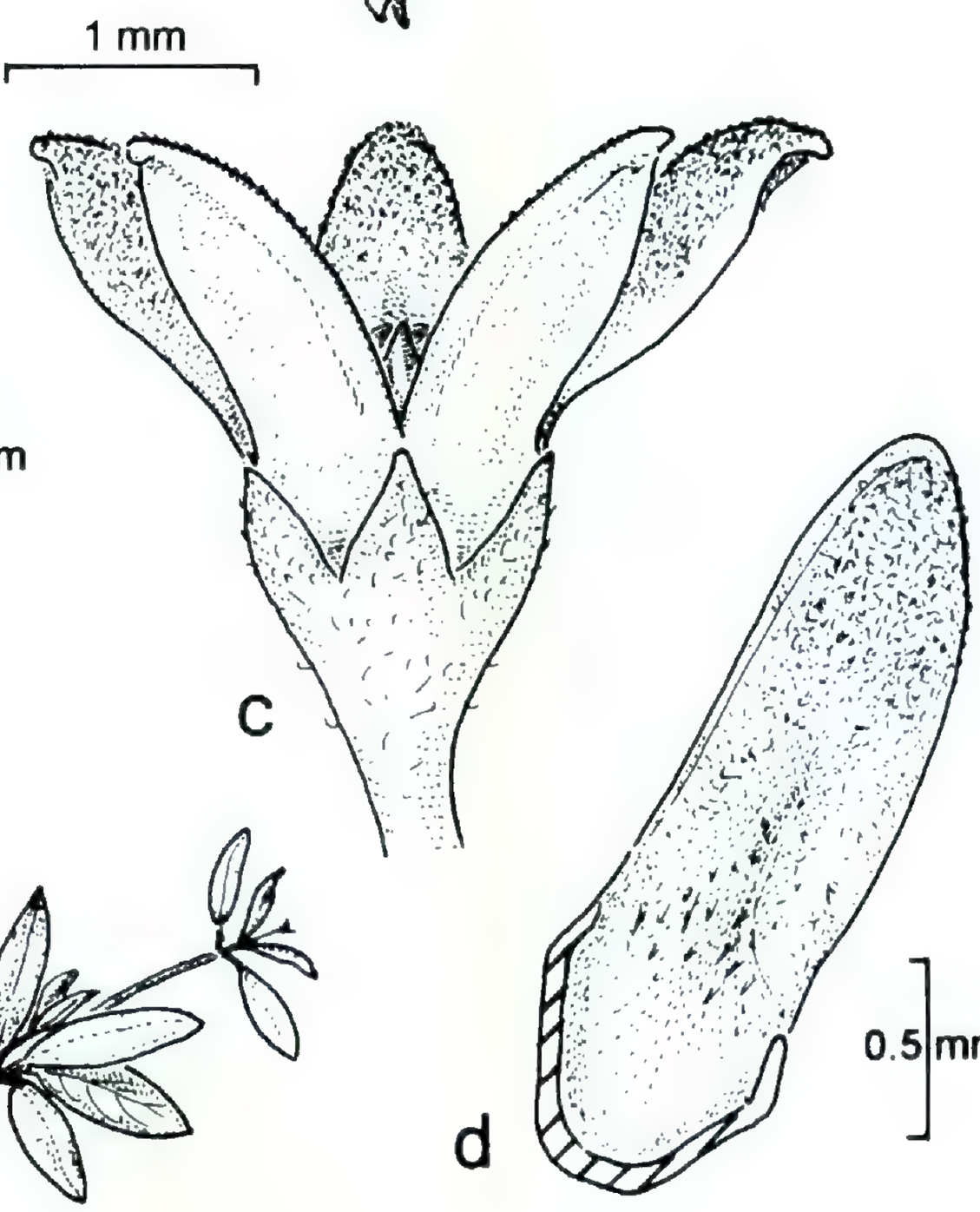
Distribution. Mexico: Sinaloa, Sonora; coastal and Sinaloan thornscrub; 0–25 m.

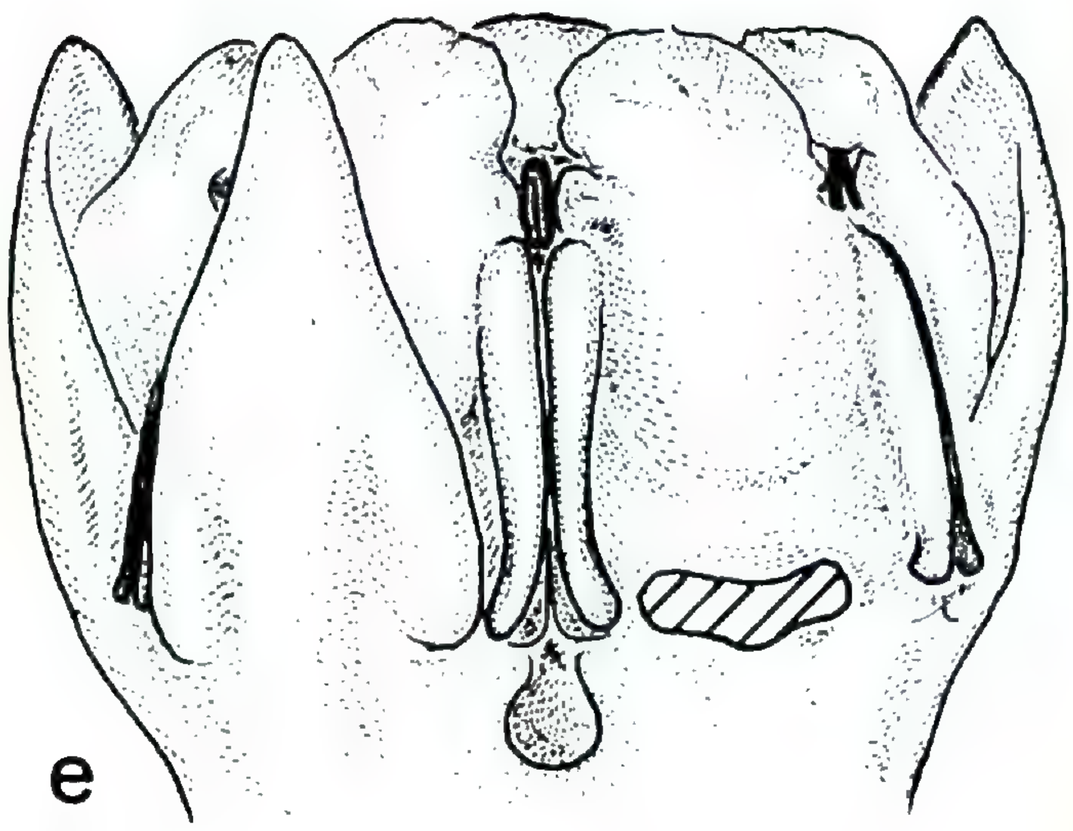
The inconspicuous indumentum of the corolla, the anther wings forming a distinct "mouth," and the very slenderly oblongoid corpusculi carrying











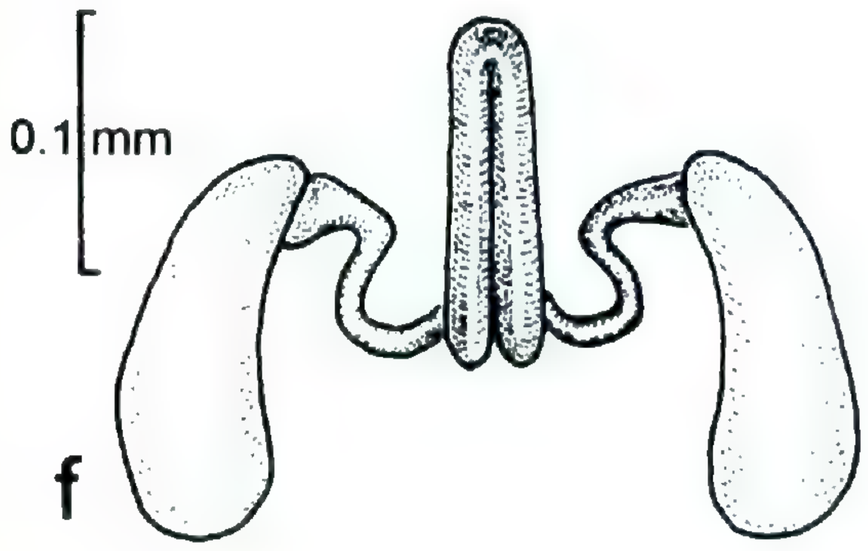


Figure 9. *Metastelma cuneatum.* —a. Shoot with follicle. —b′. Inflorescence. —c. Flower. —d. Corolla lobe, adaxial view. —e. Gynostegium and corona. —f. Pollinarium. —g. Style-head. —h″. Seed. a, c–g: *Friedman 150-95.* b: *van Devender et al. 1284.* h″: *Friedman 199-95.* Executed by U. Meve after sketch by J. Conrad.

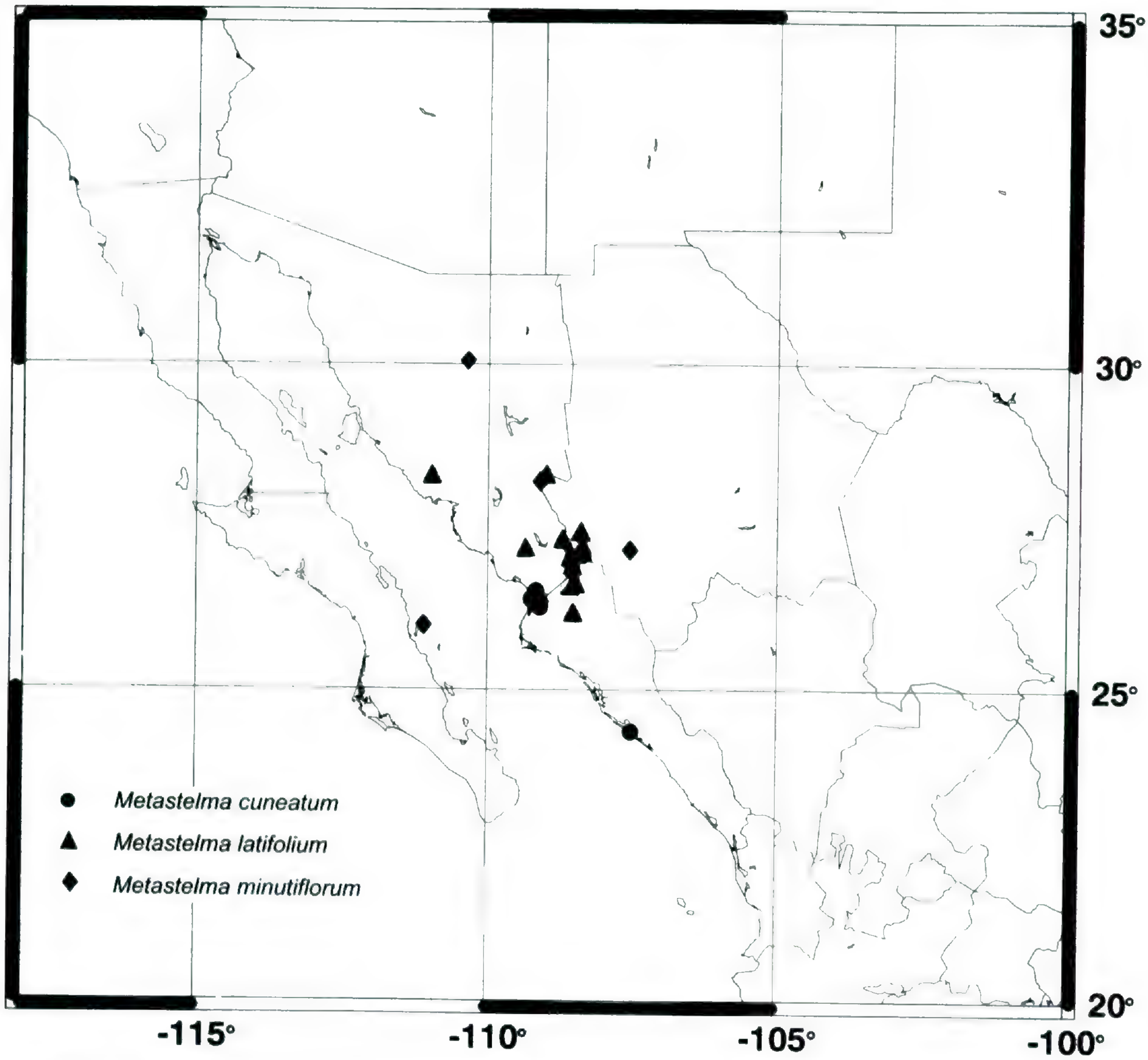


Figure 10. Distribution of *Metastelma cuneatum*, *M. latifolium*, and *M. minutiflorum*.

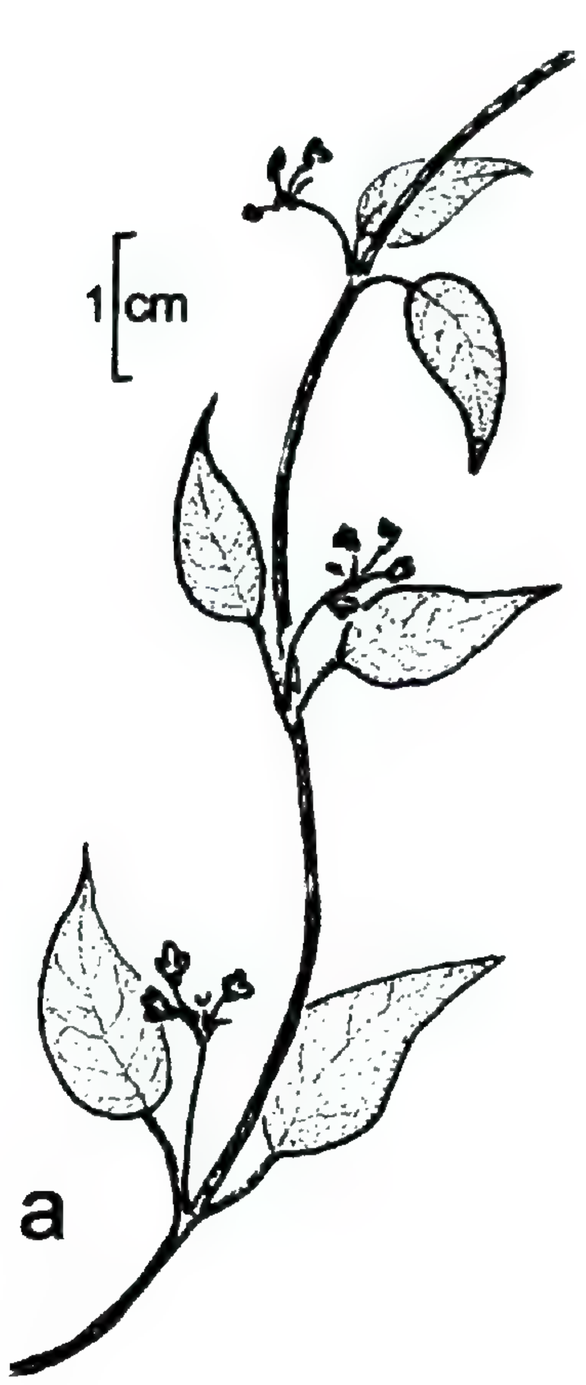
markedly s-shaped caudicles make this coastal resident an easily recognizable species.

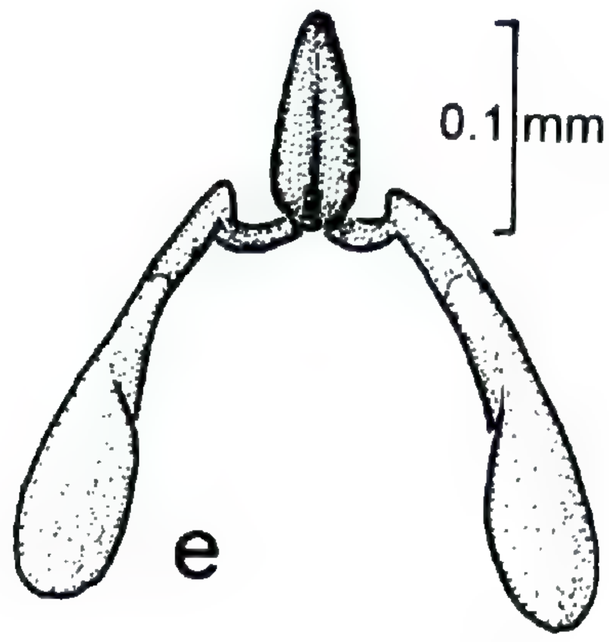
Additional specimens examined. MEXICO. **Sinaloa:** in arroyo Camahuiroa, 1.5 km NE of Camahuiroa, 15 m, 17 Jan. 1995 (fl), *Friedman 015-95* (ARIZ); nr. Arroyo Muerto, 1.5 km NNW of Camahuiroa on rd. to Las Bocas, 17 Jan. 1995 (fl), *Friedman 104-95* (ARIZ); 9.8 km W and 5 km N of Mex 15 on Las Bocas Rd., 20 Jan. 1995 (fl, fr), *Friedman 150-95* (ARIZ); 6.25 km E of Camahuiroa on rd. to Diez de Abril, 20 Jan. 1995 (fl, fr), *Friedman 199-95* (ARIZ); 4.4 km SW Ejido Tierra y Libertad, 1 km N on dirt rd., 19 Sep. 1994 (fl), *Friedman 284-94* (ARIZ). **Sonora:** along rd. to Bachoco, ca. 3.5 mi. E of Las Bocas, 24 Dec. 1995 (fl), *Fishbein 2759* (ARIZ); Las Bocas on the coast of the Gulf of California, 1 Feb. 1992 (fl, fr), *Van Devender et al. 92-133* (ARIZ); 1.5 km NNW of Camahuiroa on rd. to Las Bocas, 23 Nov. 1993 (fl, fr), *Van Devender 93-1253A* (ARIZ); 2 km W of Tierra y Libertad on northern rd. to Camahuiroa, 24 Nov. 1993 (fl), *Van Devender et al. 93-1284* (ARIZ); mouth of arroyo Masiaca, Las Bocas on the Gulf of California, 22 Sep. 1994 (fl), *Van Devender & Yetman 94-698* (ARIZ).

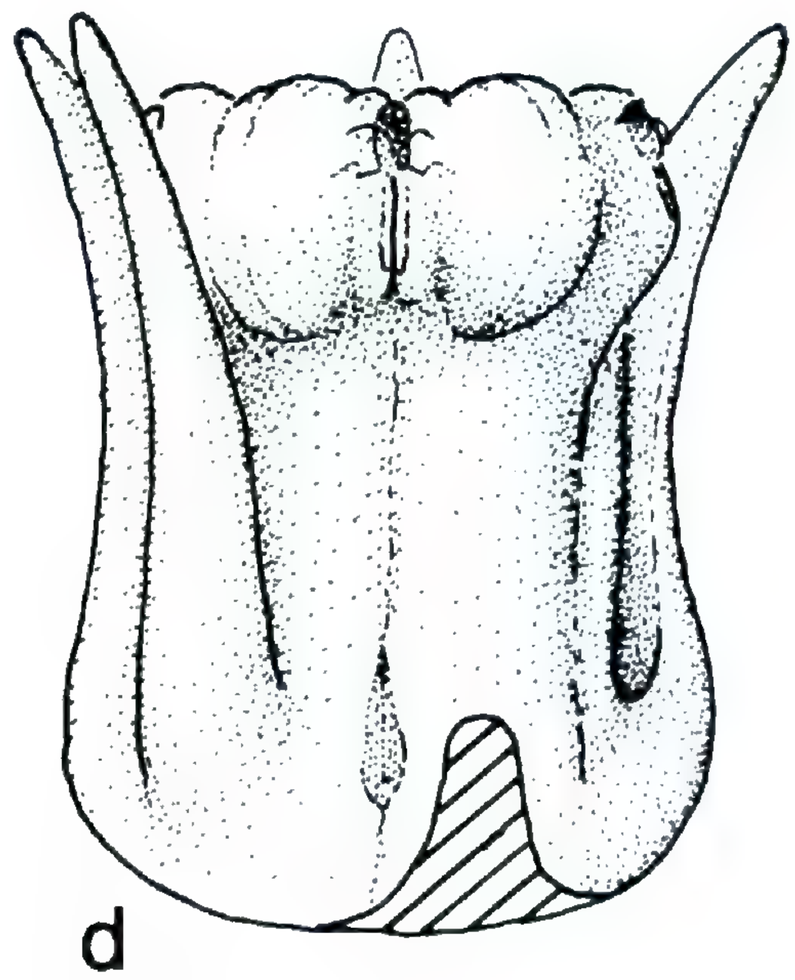
5. **Metastelma eliasianum** Dugand, Caldasia 9: 445. 1966. TYPE: Colombia. Bolívar: N of Arjona, 30–50 m, 15 Nov. 1926, *E. P. Killip & A. C. Smith 14531* (holotype, US 1.350.518 not seen; isotypes, GH not seen, NY!, P!). Figures 11a–f, 12.

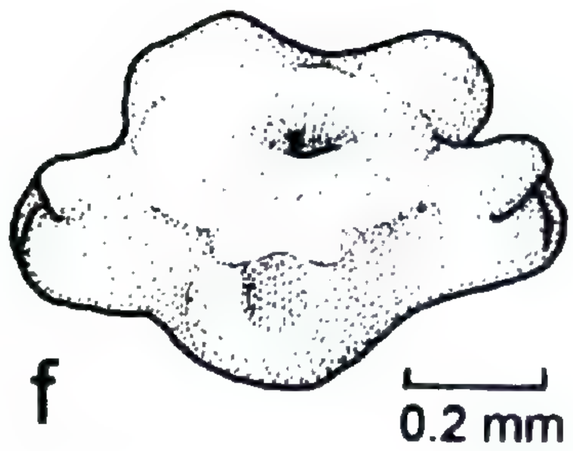
Cynanchum infimicola L. O. Williams, Ann. Missouri Bot. Gard. 55: 48. 1968. Syn. nov. *Metastelma infimicola* (L. O. Williams) W. D. Stevens, Phytologia 64: 335. 1988. TYPE: Panama. Canal Zone: K-2 road, 3 Aug. 1967, *J. D. Dwyer & S. M. V. Hayden 7540* (holotype, F!; isotype, MO not seen).

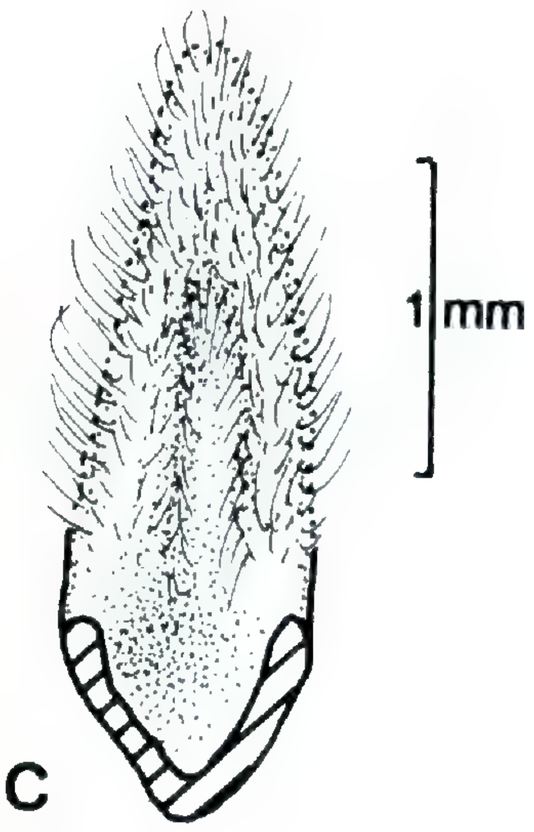
Plants ascending; *shoots* perennial, basally woody, with yellowish to brownish bark, sparsely covered along a single line with recurved trichomes, 150–250 μm long; internodes 3–7 cm long, 1–1.5 mm diam. *Leaves* with petioles 6–10 mm long, with 2 or 3 colleters at blade base; blades 25–50 × 8–30 mm, ovate, basally rounded to cu-











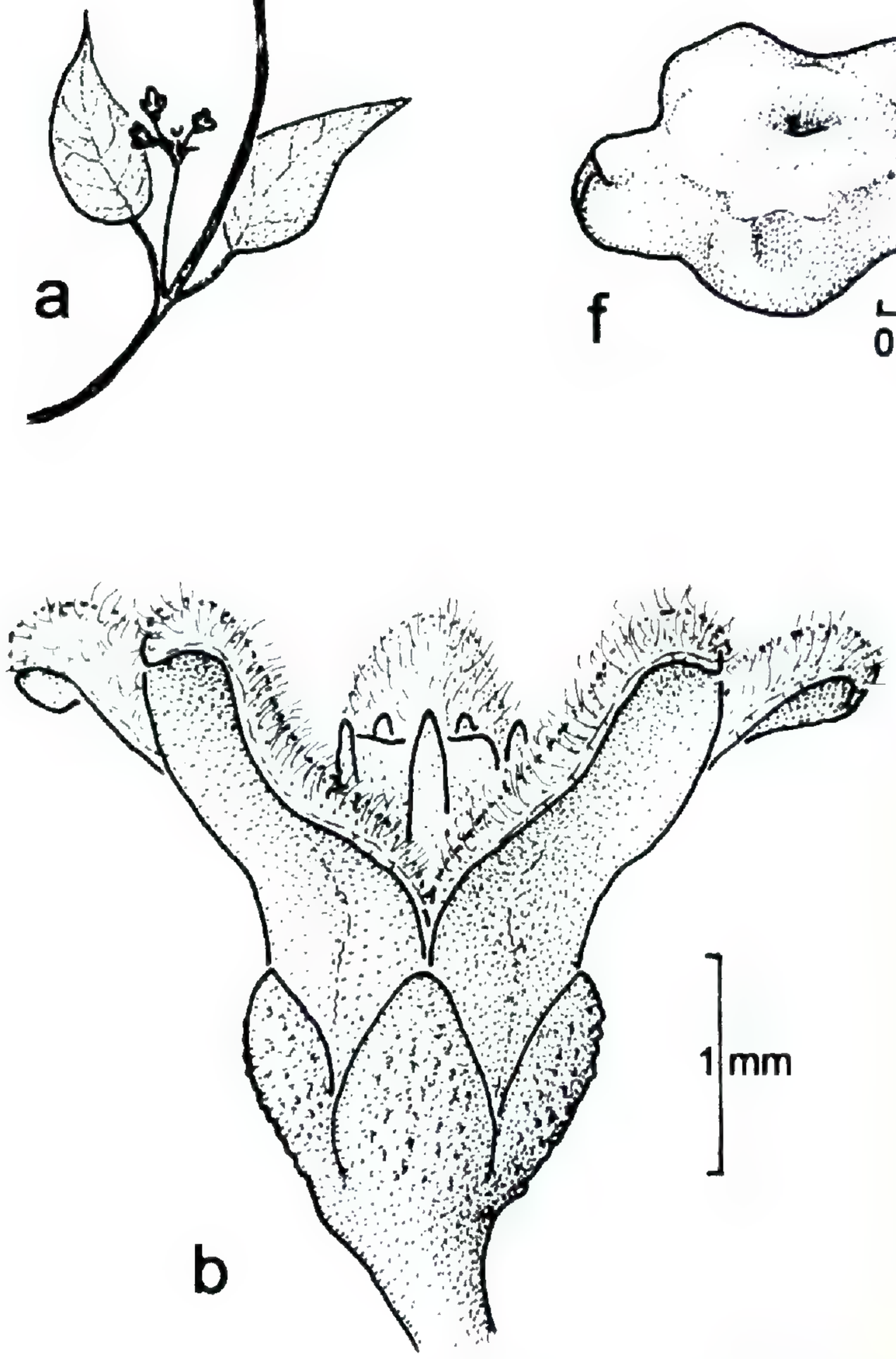


Figure 11. *Metastelma eliasianum*. —a. Shoot with inflorescences. —b. Flower. —c. Corolla lobe, adaxial view. —d. Gynostegium and corona. —e. Pollinarium. —f. Style-head. a: *Woodson, Allen & Seibert 1499*. b–f: *Duke 12414*. Drawn by J. Conrad.

neate, apically very acute, adaxially isolatedly covered only on the midrib with appressed trichomes, ca. 250 µm long, abaxially glabrous. *Inflorescences* always one per node, 4- to 7-flowered, 2 to 4 flowers open synchronously, bostrychoid; *peduncles* 5–15 mm long, sparsely to densely covered along a single line with recurved trichomes, 200–250 µm long; rachis 0–5 mm long, angular; *floral bracts* 4–5 × 3–4 mm at the base, ovate, papillose; *pedicels* 2–5 mm long, glabrous. *Floral buds* ca. 1.5 mm long, ca. 1 mm diam., cylindrical; *calyx* basally fused, cyathiform, abaxially glabrous or with a few sparse trichomes on the tube; calyx lobes 0.8–1 × 0.4–0.5 mm, ovate, apically acute; *corolla* campanulate, 2–2.5 mm long, abaxially greenish white, glabrous, adaxially white, with verrucose, 120–150 µm long trichomes on the apical parts of the lobes; lobes fused for ca. ⅓ of total corolla length, ca. 1.5 mm

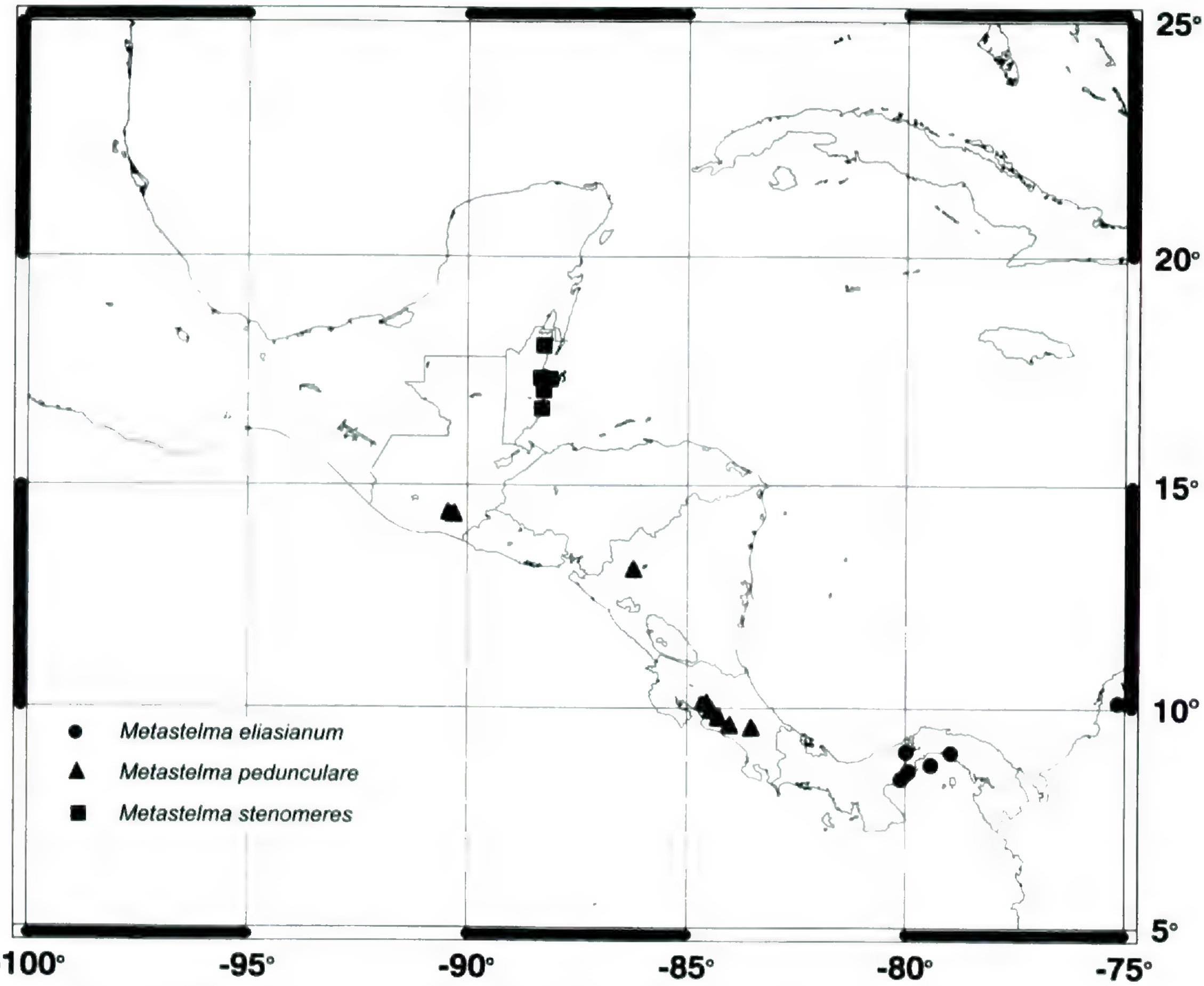


Figure 12. Distribution of *Metastelma eliasianum*, *M. pedunculare*, and *M. stenomeres*.

wide, patent, oblong, apically acute; *gynostegial corona* 1–1.2 mm long, equaling the gynostegium; lobes erect, apically reflexed, attached at the base of the stipe, laminar, oblong. *Gynostegium* ca. 0.3 mm high, ca. 0.8 mm diam., on a stipe 0.8–1 mm long; *anthers* broader than high, rectangular, abaxially planar; anther wings 300 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther; connective appendages ca. 150 μm long, ca. 300 μm wide, ovate, equaling the stamen in width, strongly inflexed; *pollinarium* with corpusculum 100 μm long, about twice as long as broad, margins of the corpuscular cleft parallel; caudicles 60–80 μm long, cylindrical, s-shaped, convex-concave; pollinia apically attached to the caudicles, ca. 350 μm long, ca. 70 μm wide, ovate in cross section, clavate; *style-head* white, ca. 0.7 mm diam., ca. 0.2 mm high, flat. *Follicles* one per flower, 50–60 mm long, 3–4 mm diam., narrowly obclavate to fusiform, terete, apically strongly beaked, wingless, medium brown, glabrous; *seeds* unknown.

Phenology. Collected in flower in May and from July to September.

Distribution. Colombia. Panama: Coclé, Canal Zone, Panamá; savanna and thickets; 0–200 m, one record (*Tyson et al. 3962*, NY) from 700 m.

Metastelma eliasianum is most closely related to *M. pedunculare* and shares with it the long stipe, the tiny, ca. 0.3 mm high gynostegium, and a similar pollinarium structure. However, the long corona lobes of *M. eliasianum* originate at the base of the stipe, while the shorter corona lobes of *M. pedunculare* originate just underneath the gynostegium. *Metastelma eliasianum* thus takes an intermediate position both in corona morphology and geographical distribution between the truly Central American *M. pedunculare* and the South American *M. parviflorum*, in which the attachment of the corona lobes has moved even further away from the gynostegium and onto the base of the corolla.

Based on specimen records, *Metastelma eliasianum* might be more widely distributed in South America, but this is beyond the scope of the present revision.

Additional specimens examined. PANAMA. **Coclé:** betw. Las Margeritas & El Valle, 15 July 1938 (fl), *Woodson et al. 1263* (NY). **Panamá:** 2 mi. S of El Valle, 11 May 1966 (fl), *Tyson et al. 3962* (NY); nr. Rio Mar, 13 July 1967 (fl), *Duke 12414* (NY, WIS); Taboga Island, 1 Sep. 1962 (fl), *Dwyer 2809* (NY), 20 May 1911 (fl), *Pittier 3539* (NY), 23 July 1938 (fl), *Woodson et al. 1499* (NY).

6. Metastelma latifolium Rose, Contr. U.S. Natl. Herb. 1: 106. 1891. TYPE: Mexico. Sonora: Alamos, 16 Sep. 1890, *E. Palmer 665* (holotype, US not seen; isotypes, GH–2 not seen, NY!). Figures 10, 13a–f.

Plants ascending; *shoots* perennial, basally woody, with blackish brown bark, sparsely covered along a single line with flexuous trichomes, 350–450 μm long; internodes 2.5–6 cm long, 1 mm diam. *Leaves* with petioles 3–5 mm long, with 2 colleters at blade base; blades 25–55 × 7–15 mm, ovate, basally obtuse, apically acute to acuminate, adaxially sparsely covered only on veins and margins with flexuous trichomes, 300–400 μm long, abaxially isolatedly covered, only on the midrib with flexuous trichomes, 300–400 μm long. *Inflorescences* always one per node, 2- to 12-flowered, 2 to 6 flowers open synchronously, sciadioidal (sometimes a little elongated); *peduncles* 1–4 mm long, densely covered along a single line with flexuous trichomes, 300–400 μm long; *floral bracts* 0.5–0.7 × 0.2–0.3 mm at the base, ovate to triangular, glabrous; *pedicels* 2–5 mm long, glabrous. *Floral buds* 1.6–1.8 mm long, 0.8–1.1 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially glabrous; calyx lobes 0.8–0.9 × 0.4–0.5 mm, ovate, apically acute; *corolla* campanulate, 1.7–2 mm long, abaxially white, glabrous, adaxially white, with verrucose trichomes 100–120 μm long on the apical and on the lateral parts of the lobes, and with downward-directed smooth trichomes 150–200 μm long on the central parts of the lobes; lobes basally fused, 0.4–0.6 mm wide, erect to patent, ovate, apically acute; *gynostegial corona* 0.5–0.6 mm long, shorter than to equaling the gynostegium; lobes erect, laminar, oblong. *Gynostegium* 0.7–0.9 mm high, 0.9–1 mm diam., subsessile; *anthers* about as high as broad, rectangular, abaxially planar; anther wings 350–400 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other; connective appendages ca. 250 μm long, ca. 350 μm wide, ovate, equaling the stamen in width, slightly to strongly inflexed; *pollinarium* with corpusculum ca. 120 μm long, between 1.5 times and twice as long as broad, ovoid; caudicles 50–60 μm long, cylindrical, geniculate, thickened at the insertion of the pollinium; pollinia subapically attached to the caudicles, ca. 140 μm long, 50–60 μm wide, ovate in cross section, oblongoid; *style-head* ca. 0.7 mm diam., 0.3–0.4 mm high, upper part 0–0.2 mm high, shorter than to equaling the lower part, flat to umbonate. *Follicles* and *seeds* unknown.

Phenology. Collected in flower in March and April and from August to October.

Distribution. Mexico: Chihuahua, Sonora; open places in mixed deciduous hardwood forests and tropical deciduous forests; 250–1200 m.

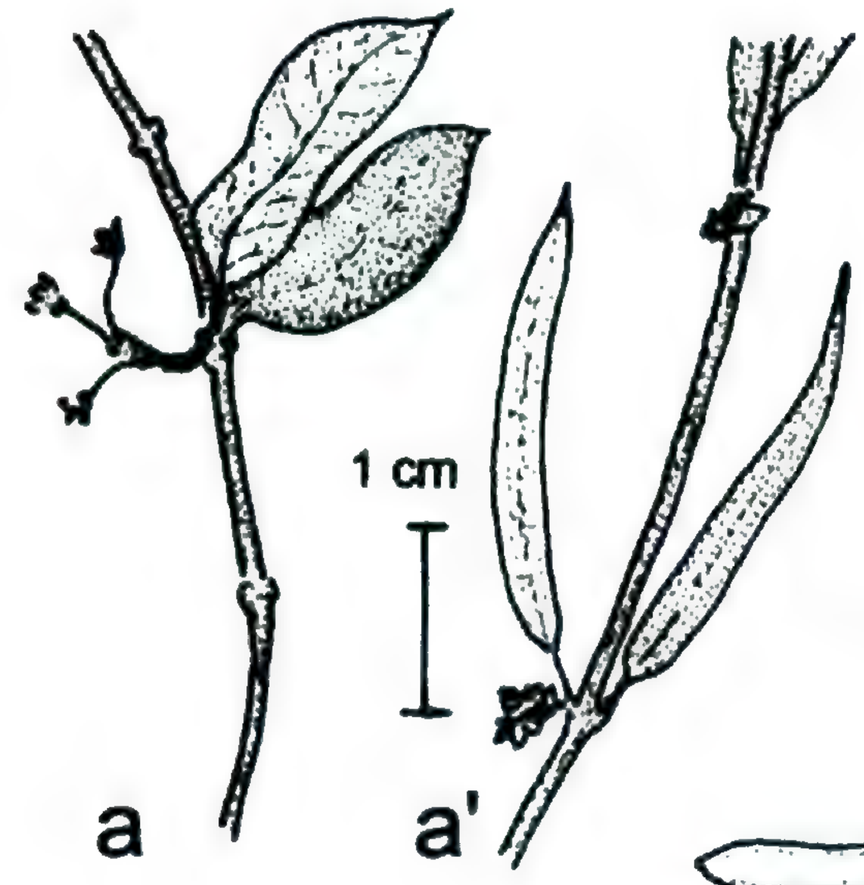
Literature and illustrations. Wiggins (1940: 82, pl. 18).

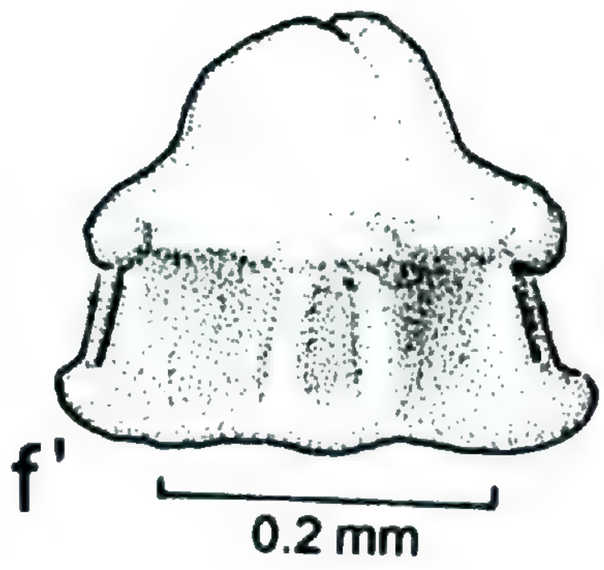
Metastelma latifolium and *M. minutifolium* constitute a pair of closely related, very small-flowered (corolla less than 2 mm long) species with different ecological preferences. *Metastelma latifolium*, characterized by ovate, apiculate leaves, shoots with one line of trichomes, pedunculate inflorescences, ovoid to oblongoid pollinia and flat to umbonate style-heads, is an inland and upland species, while *M. minutiflorum*, characterized by linear to slenderly lanceolate leaves, shoots with two lines of trichomes, subsessile inflorescences, reniform pollinia, and conical style-heads, prefers habitats close to the coast. A detailed analyis of the tiny pollinaria and the style-heads is necessary for secure determination (cf. Fig. 13).

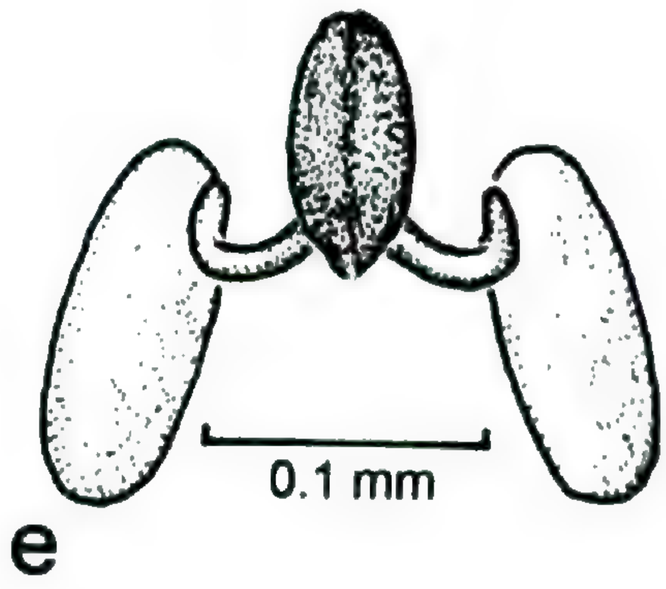
Additional specimens examined. MEXICO. **Chihuahua:** Guasaremos, Rio Mayo, 10 Aug. 1936 (fl), *Gentry 2373* (ARIZ). **Sonora:** ca. 40 mi. NE of Alamos, 2 mi. S of Chinacas, 12 Aug. 1980 (fl), *Lehto 24882* (ARIZ); Cerros Colorados, 3–4 km E of El Tabelo on rd. to Piedras Verdes, 29 Oct. 1995 (fl), *Van Devender et al. 95-1189* (ARIZ); E of Nuri & W of Tesopaco, along new rd., 13 Aug. 1976 (fl), *Goldberg 76-322* (ARIZ); Sierra de Alamos, ca. 2 km S of Alamos, 31 Aug. 1996 (fl), *Steinmann 955* (ARIZ, NY); Sierra de Alamos, E of Arroyo Agua Escondida, 20 Aug. 1994 (fl), *Fishbein et al. 1903* (ARIZ); Sierra de Alamos, Cañon Chapotes 19 Mar. 1994 (fl), *Fishbein et al. 1606* (ARIZ); along Hwy. 16, 3.5 mi. E of Tepoca, 11 mi. E of Puerto de la Cruz, 6 Sep. 1995 (fl), *Fishbein 2460* (ARIZ); Rancho las Uvalamas, 25 Aug. 1990 (fl), *Martin & McWorther s.n.* (NY); 26.9 km SE of Rio Yaqui on MEX 16 (Rancho La Mula), 21 Sep. 1997 (fl), *Reina et al. 97-1087* (ARIZ, LL).

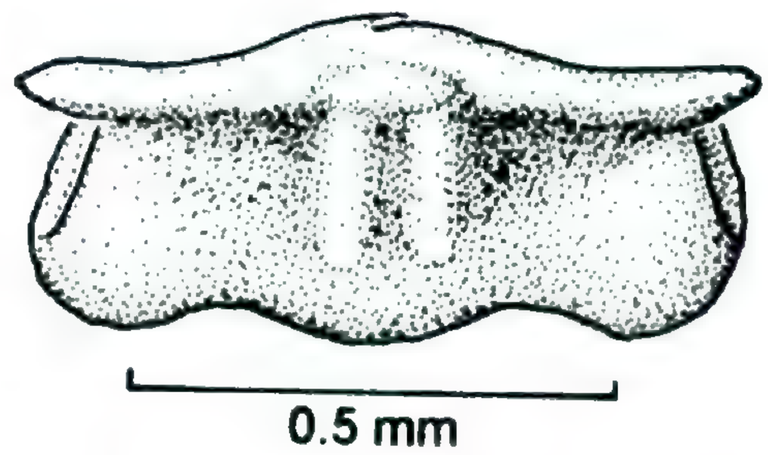
7. Metastelma longicoronatum (L. O. Williams) Liede & Meve, Novon 7: 42. 1997. *Cynanchum longicoronatum* L. O. Williams, Fieldiana, Bot. 32: 37. 1968. TYPE: Mexico. Chiapas: steep slope with *Quercus* along Mexican Hwy. 190, 3 mi. S of La Trinitaria, alt. 5100 ft., 14 Oct. 1965, *D. E. Breedlove & P. H. Raven 13199* (holotype, F!; isotype, DS not seen). Figures 14a–f, 15.

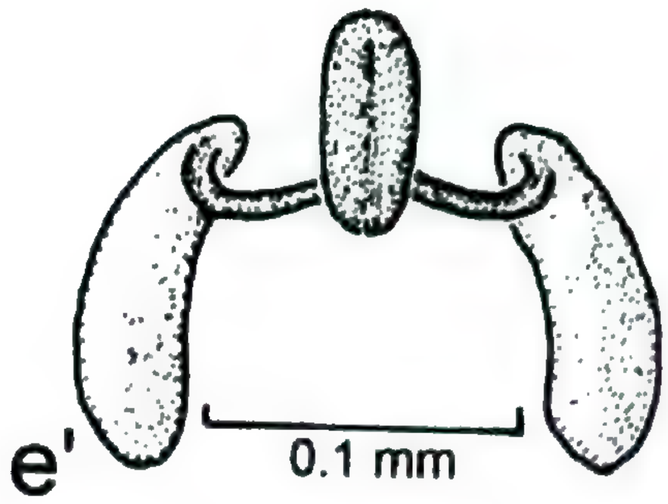
Plants ascending; *shoots* perennial, basally

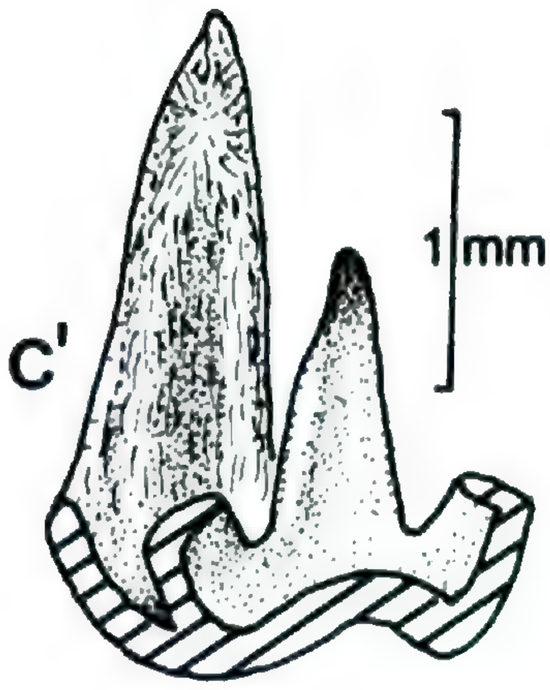


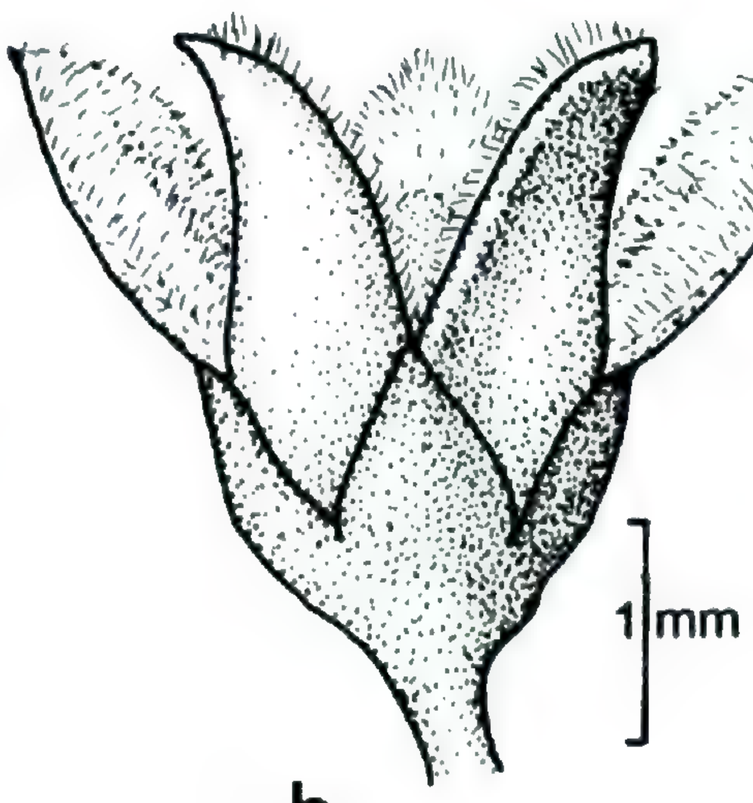


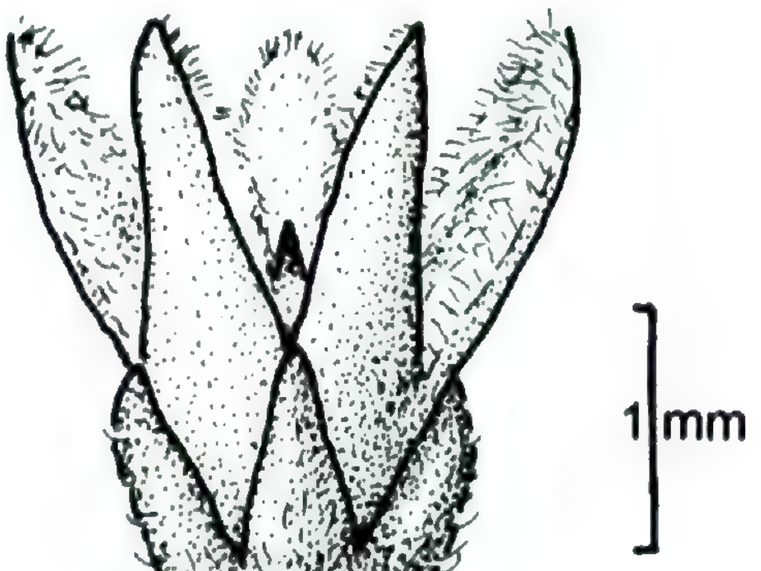


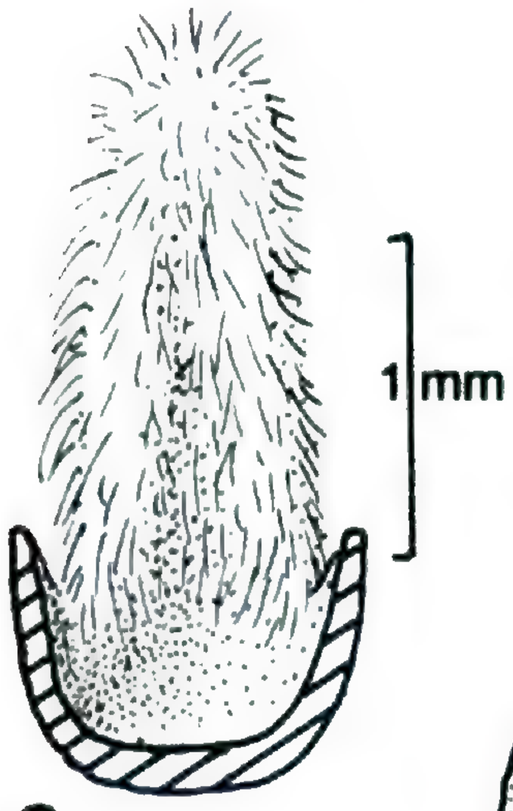


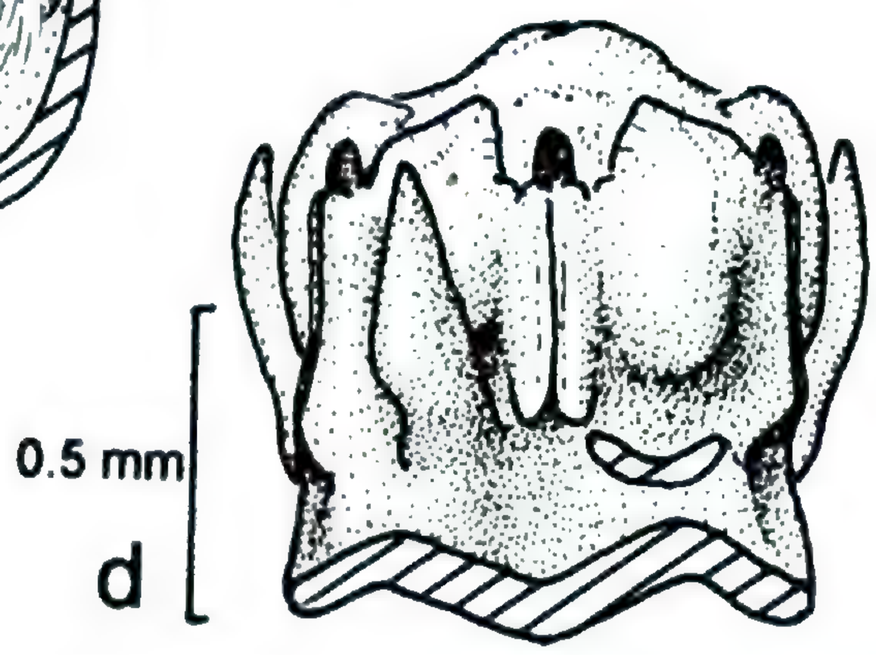












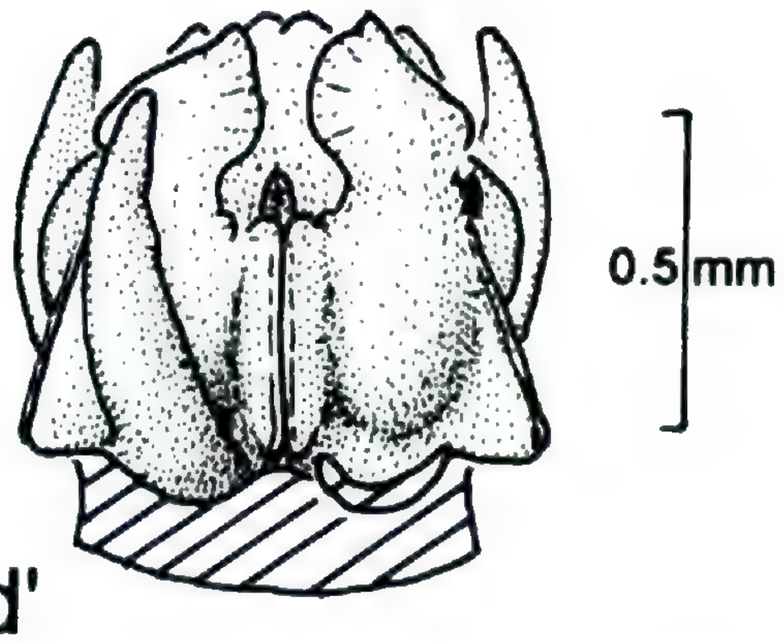
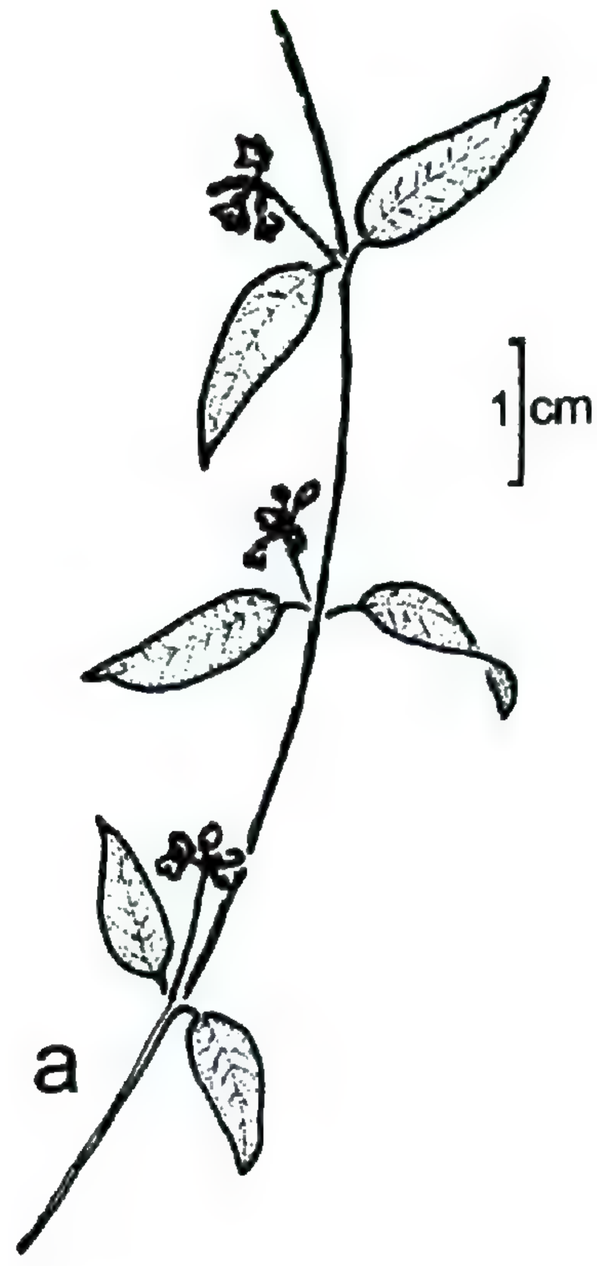
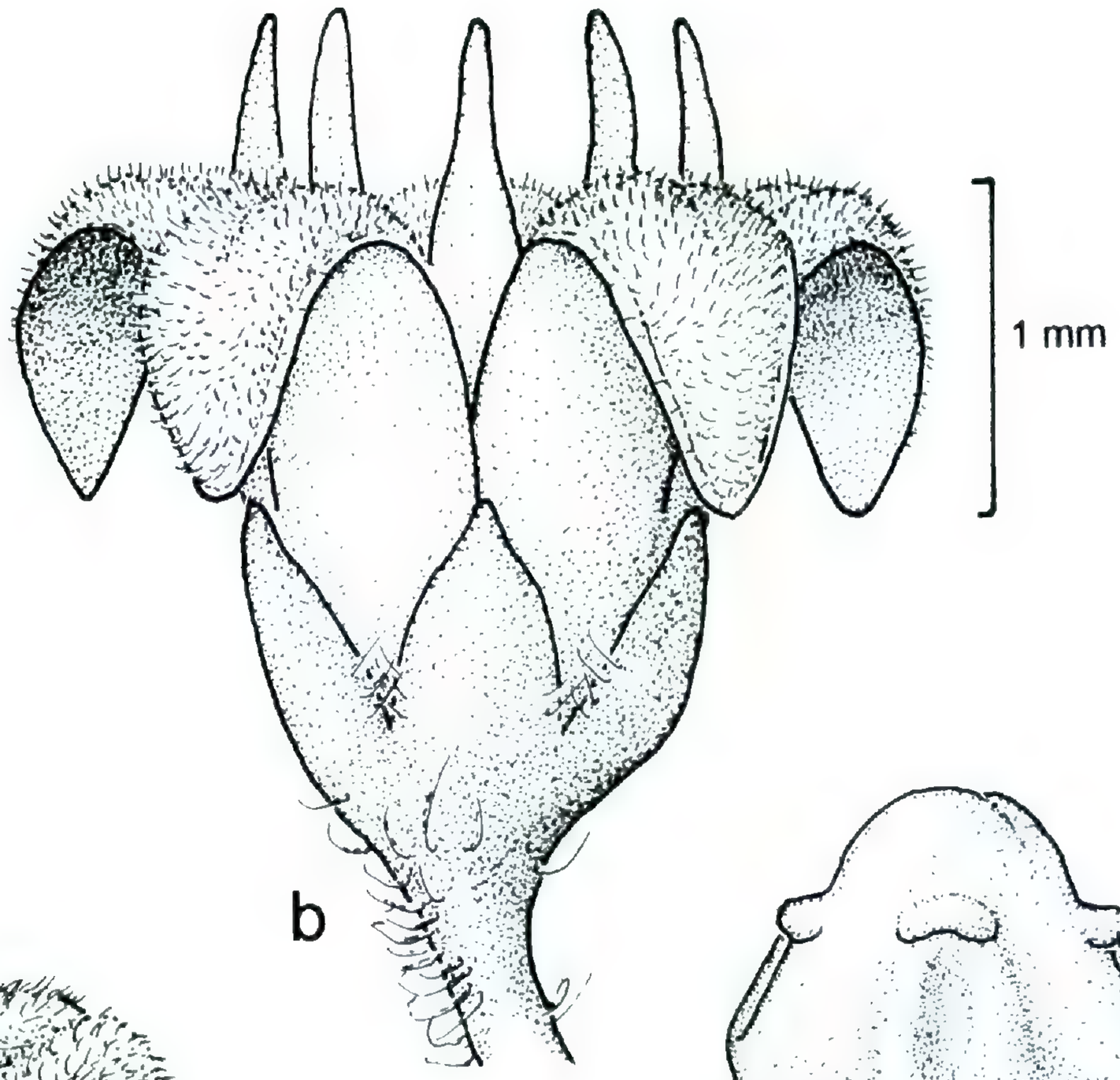
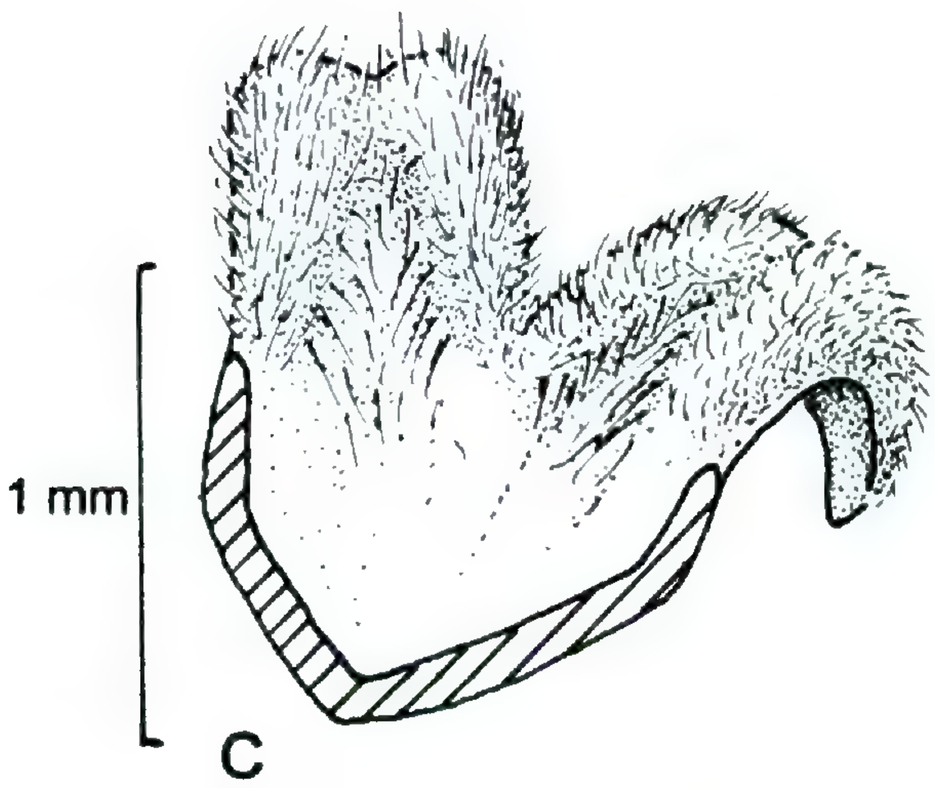
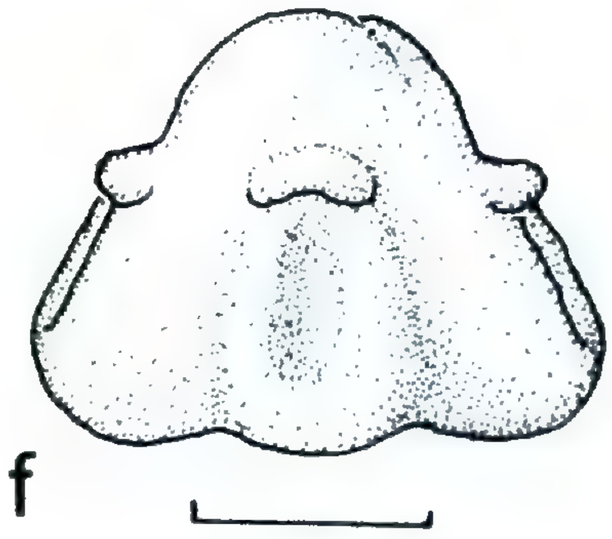


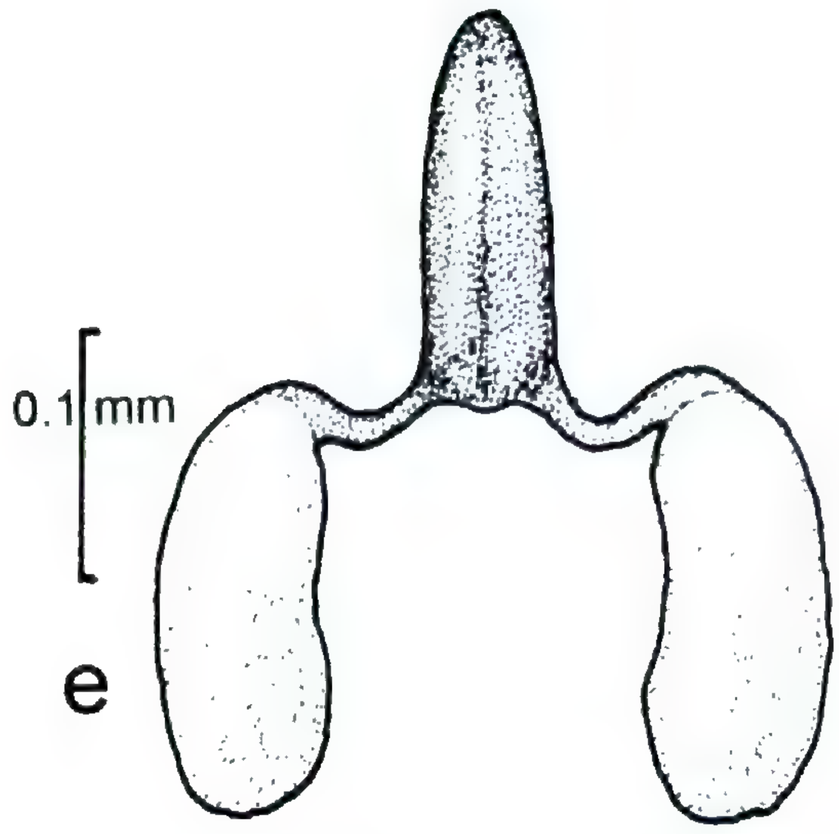
Figure 13. *Metastelma latifolium* and *Metastelma minutiflorum*. a–f: *Metastelma latifolium*. a: *Palmer 665*, b–f: *Steinman 955*. a'–f': *Metastelma minutiflorum*, *Gentry 4857*. —a, a'. Shoot with inflorescence. —b, b'. Flower. —c, c'. Corolla lobe, adaxial view. —d, d'. Gynostegium and corona. —e, e'. Pollinarium. —f, f'. Style-head. Drawn by J. Conrad.











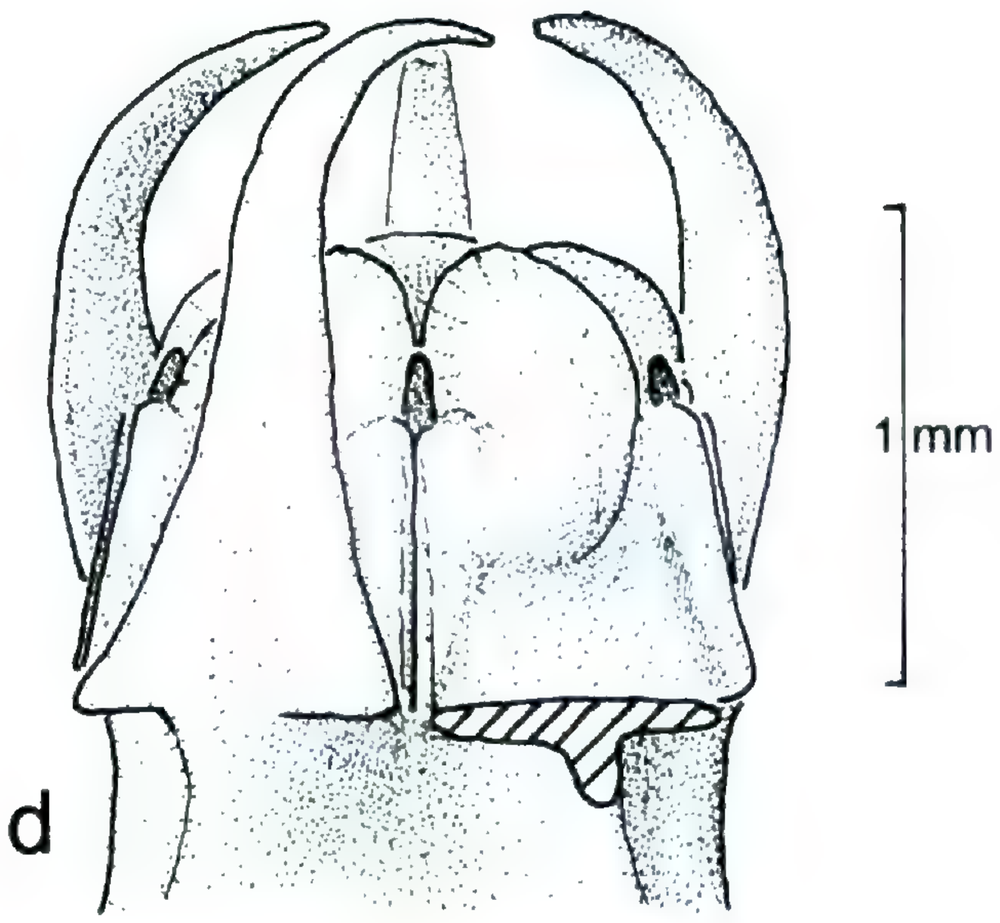


Figure 14. *Metastelma longicoronatum*. —a. Shoot with inflorescences. —b. Flower. —c. Corolla lobe, adaxial view. —d. Gynostegium and corona. —e. Pollinarium. —f. Style-head. *Breedlove & Raven 13199*. Drawn by J. Conrad.

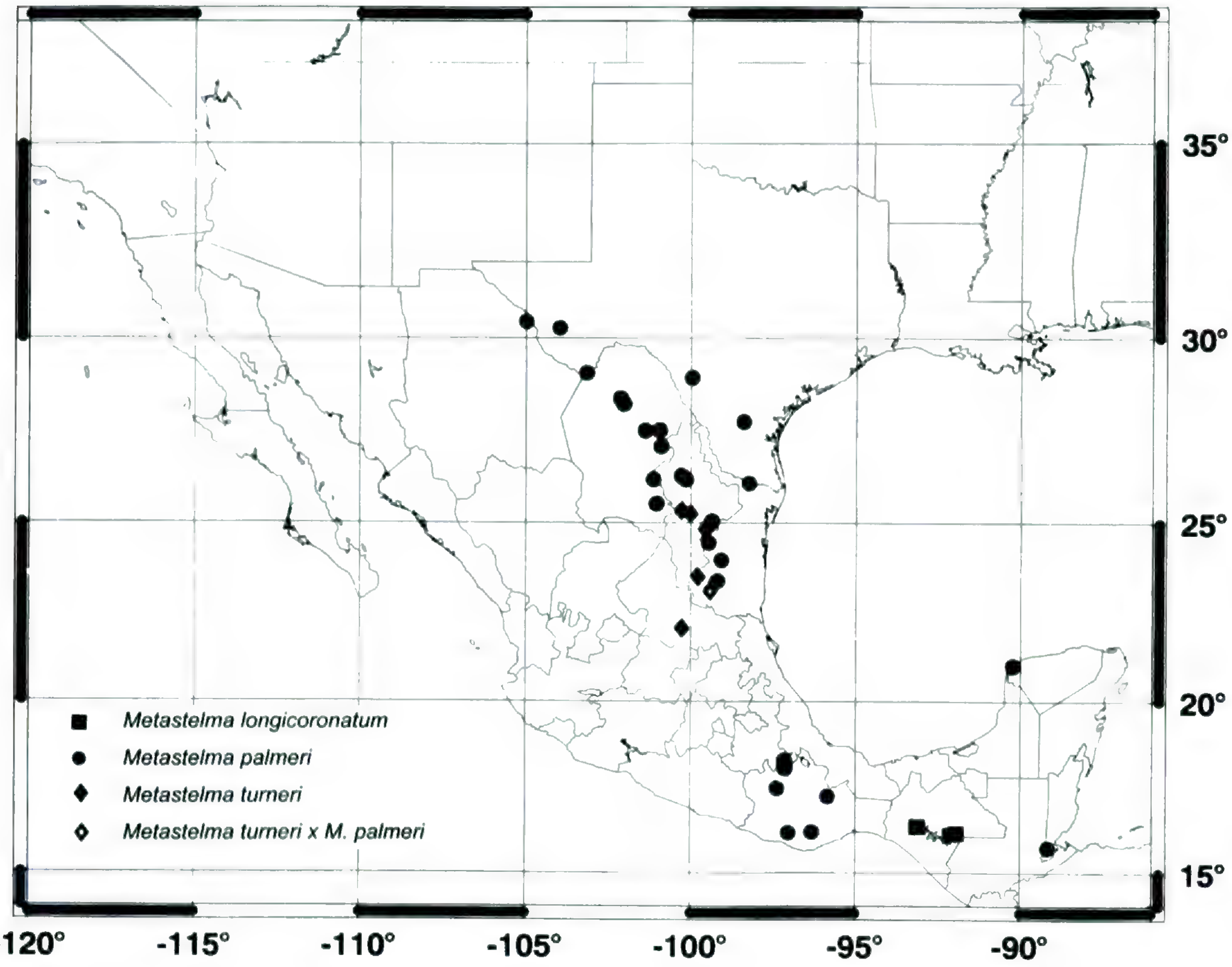


Figure 15. Distribution of *Metastelma longicoronatum*, *M. palmeri*, and *M. turneri*.

woody, with dark brownish bark, densely covered along a single line with flexuous trichomes, 250–300 μm long; internodes 2–6 cm long, 1 mm diam. *Leaves* with petioles 3–5 mm long, with 2 colleters at blade base; blades 20–40 × 6–12 mm, ovate, basally rounded, apically acute to acuminate, adaxially isolatedly covered mainly on veins and margins with appressed trichomes, 250–300 μm long, abaxially glabrous. *Inflorescences* always one per node, 4- to 8-flowered, 3 to 5 flowers open synchronously, sciadioidal; *peduncles* 3–15 mm long, densely covered along a single line with flexuous trichomes, 150–200 μm long; *floral bracts* 0.4–0.5 × 0.2–0.3 mm at the base, ovate, with trichomes on the surface; *pedicels* 2–3 mm long, densely covered along a single line with recurved trichomes, 150–200 μm long. *Floral buds* 2–2.2 mm long, 1–1.2 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially with trichomes (mainly on the tube); calyx lobes 0.8–1 × 0.4–0.5 mm, ovate, apically acute; *corolla* campanulate, 2.5–3 mm long, abaxially white, glabrous, adaxially white, with verrucose trichomes, 100–150 μm long, on the apical and on the lateral parts of the lobes and with smooth, downward-directed trichomes, 150–200 μm long on the central parts of the lobes; lobes basally fused to ca. ⅓ of total corolla length, ca. 1 mm wide, patent, ovate, apically acute, recurved; *gynostegial corona* 2 mm long, longer than the gynostegium; lobes erect, apically slightly connivent, attached at the base of the stipe, laminar, elongatedly triangular and with a conspicuously winged base. *Gynostegium* ca. 0.8 mm high, ca. 0.8 mm diam., on a stipe ca. 0.6 mm long; *anthers* about as high as broad, rectangular, abaxially planar; anther wings 0.6 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther; connective appendages ca. 400 μm long, ca. 300 μm wide, ovate, narrower than the stamen, slightly inflexed; *pollinarium* with corpusculum ca. 160 μm long, more than twice as long as broad, elliptic; caudicles ca. 70 μm long, flattened, slightly s-shaped, concave-convex; pollinia apically attached to the caudicles, ca. 180 μm long, ca. 80 μm wide, ovoid; *style-head* white, ca. 0.5 mm diam., ca. 0.4 mm high, upper part ca. 0.15

mm high, shorter than the lower part, depressed-conical. *Follicles* and *seeds* unknown.

Phenology. Collected in flower in July, August, and October.

Distribution. Mexico: Chiapas; cliff faces and limestone bluffs with seasonal evergreen forest; 1300–1700 m.

Metastelma longicoronatum is a rare species endemic to Chiapas. The elongated triangular shape of the corona lobes with a conspicuously winged, almost hastate base, is unmistakable.

Additional specimens examined. MEXICO. **Chiapas:** El Sumidera, 22 km N of Tuxtla Gutiérrez, 19 Aug. 1972 (fl), *Breedlove 27183* (TEX); Comitán de Dominguez, 21 July 1989 (fl), *Liede & Conrad 2557* (UBT).

8. Metastelma mexicanum (Brandegee) Fishbein & R. A. Levin, Madroño 44: 270. 1997. Basionym: *Melinia mexicana* Brandegee, Zoë 5: 216. 1905. *Basistelma mexicanum* (Brandegee) Bartlett, Proc. Amer. Acad. Sci. 44: 632. 1909. TYPE: Mexico. Sinaloa: ca. 30 mi. E of Culiacan, near Durango border, Cerro Colorado, 3 Nov. 1904, *T. S. Brandegee s.n.* (holotype, GH not seen). Figures 3, 16a–k.

Cynanchum wigginsii Shinners, Sida 1: 365. 1964. Basionym: *Metastelma angustifolium* Torr., Report on the U.S. & Mexican Boundary Survey 2: 159. 1859, non *Metastelma angustifolium* Turcz., Bjull. Moskovsk. Obsc. Isp. Prir., Otd. Biol. 25: 314. 1852. *Melinia angustifolia* (Torr.) A. Gray, Proc. Amer. Acad. Sci. 12: 73. 1877. *Pattalias angustifolius* (Torr.) S. Watson, Proc. Amer. Acad. Sci. 24: 60. 1889. *Basistelma angustifolium* (Torr.) Bartlett, Proc. Amer. Acad. Arts 44: 632. 1909. TYPE: Mexico. Sonora: Santa Cruz, 1851, *C. Wright 1677* (holotype, NY!; isotypes, GH!, MO not seen).

Plants ascending, to 300 cm high; *subterranean organs* constituting a woody rootstock; *shoots* perennial, basally corky, densely covered along a single line with recurved trichomes, 200–250 μm long; internodes 2–3.5 cm long, 0.5–1 mm diam. *Leaves* with petioles 1–2 mm long, with 0 to 2 colleters at blade base; blades 20–40 × 1–2 mm, linear, basally cuneate, apically acute, marginally revolute when dry, adaxially isolatedly to sparsely covered on the midrib and the margins with recurved trichomes, 200–250 μm long, abaxially glabrous. *Inflorescences* always one per node, 2- to 4-flowered, all flowers open synchronously, sciadioidal; *peduncles* 0–2 mm long, densely covered along a single line with recurved trichomes, 150–200 μm long; *floral bracts* 2–3 × 0.2–0.3 mm at the base, very elongate triangular, with trichomes on the surface; *pedicels* 2–3 mm long, densely covered along a single line with recurved trichomes, 150–200 μm long. *Floral buds* ca. 3 mm long, ca. 1.5 mm diam., ovoid; *calyx* basally fused; calyx lobes 2.2–3 × 0.3–0.4 mm, very elongatedly triangular, apically acute, abaxially with recurved trichomes; *corolla* campanulate, 2.5–3.5 mm long, abaxially white, glabrous, adaxially white, adaxially with verrucose trichomes to 50 μm long on the apical parts of the lobes and with smooth trichomes, 150 μm long, forming a tuft at the entrance of the tube; lobes basally fused, ca. 1 mm wide, patent, ovate, apically acute, recurved; *gynostegial corona* ca. 1.2 mm long, shorter than the gynostegium; lobes erect, attached at the base of the stipe, attached with a distinct hook-shaped base, laminar, obovate. *Gynostegium* 1.4–1.6 mm high, 1–1.2 mm diam., on a stipe 0.4 mm long; *anthers* broader than high, deltoid, abaxially planar; anther wings 300–400 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther; connective appendages 900–1000 μm long, 400–500 μm wide, ovate, narrower than the stamen, erect; *pollinarium* with corpusculum ca. 300 μm long, more than twice as long as broad, elliptic; caudicles ca. 150 μm long, flattened, convexly recurved, horizontal, ellipsoid-rectangular; pollinia subapically attached to the caudicles, ca. 300 μm long, ca. 150 μm wide, ovate in cross section, oblongoid; *style-head* white, ca. 0.8 mm diam., ca. 1.2 mm high, upper part ca. 0.8 mm high, longer than the lower part, elongated-conical to obinfundibuliform. *Follicles* one per flower, erect, 50–60 mm long, 4–5 mm diam., fusiform, obtusely deltate in cross section, apically strongly beaked, medium brown, longitudinally grooved; *seeds* ovate, light brown, seta side tuberculate, papillose with regularly arranged papillae, aseta side sculptured with longitudinal ridges, with regularly arranged papillae, marginally wingless, denticulate; coma 10–15 mm long.

Phenology. Collected in flower from June to August and in October; in fruit in October.

Distribution. Mexico: Sonora; U.S.A.: Arizona, New Mexico; open rocky slopes in pine-oak woodlands, tropical deciduous forest; 900–1550 m.

Metastelma mexicanum is probably the most distinctive *Metastelma* species in the southwestern U.S.A. and Central America. It possesses extremely large sepals reaching the length of the corolla in some specimens (e.g., *Jenkins 93-88*, ARIZ). The corona is basally fused to the stipe but also to the corolla base, a character shared only with a few South American *Metastelma* species (e.g., *M. par-*

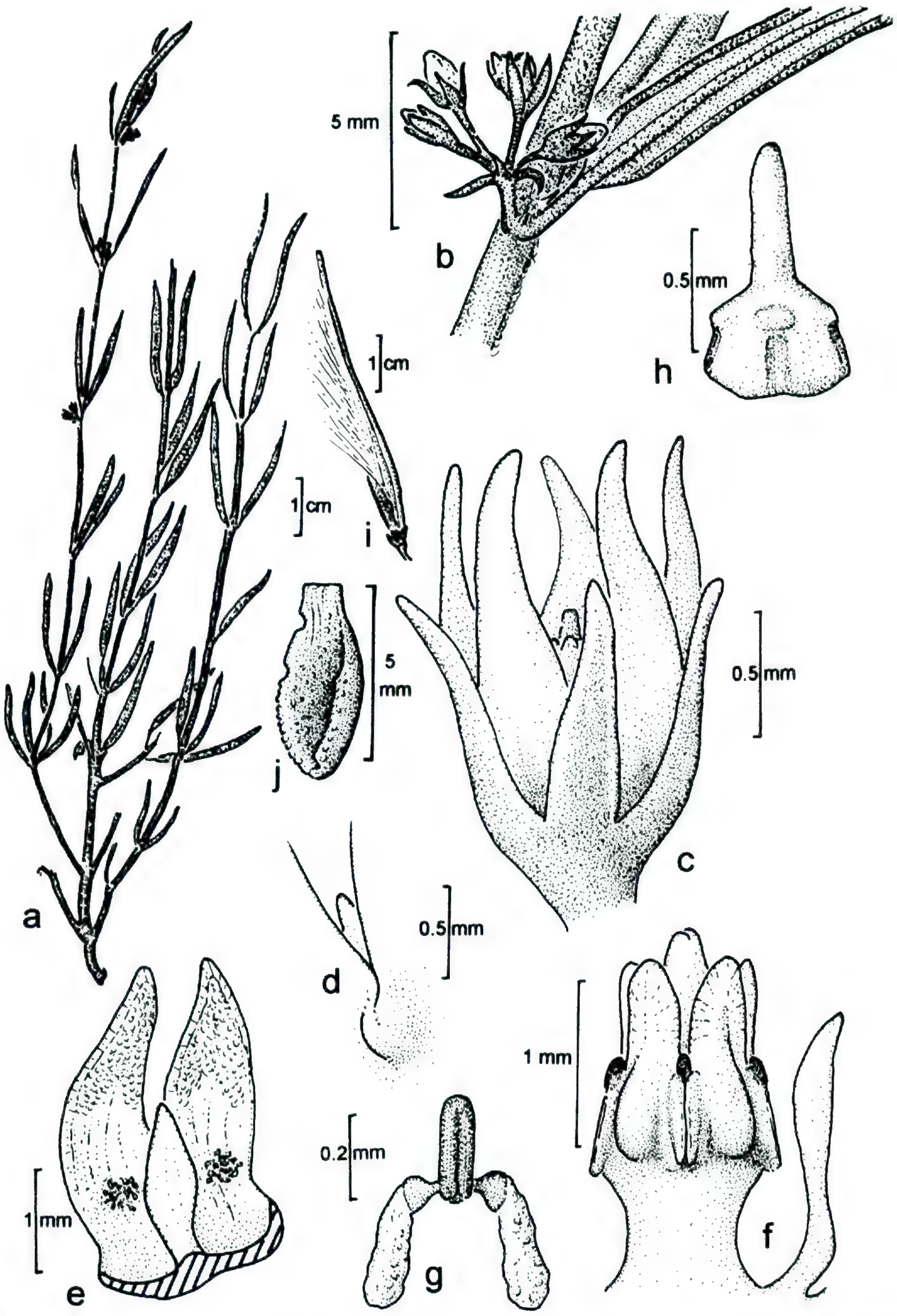


Figure 16. *Metastelma mexicanum.* —a. Habit. —b. Inflorescence. —c. Flower. —d. Sinus of corolla lobes, abaxial view. —e. Two corolla lobes and one corona lobe, adaxial view. —f. Gynostegium. —g. Pollinarium. —h. Style-head. —i. Follicle. —j. Seed. a–h: *Spellenberg & Repass 5353.* i–k: *Van Devender et al. s.n.* Drawn by J. Conrad.

riflorum, see introduction). Most diagnostic, however, are the large, erect anther appendages, which are nearly as long as the elongated style-head. For a discussion of infraspecific variation, see Fishbein and Levin (1997). The closest relative of *M. mexicanum* is probably *M. arizonicum*, judging from gynostegium structure.

Additional specimens examined. MEXICO. **Sonora:** Sierra Saguaribo, along road from Saguaribo to El Chiribo, 23 Aug. 1993 (fl), *Fishbein et al. 1362* (ARIZ); Sierra Saguaribo, Mesa Mesopaco, above La Vinateria, ca. 35 km NE of Alamos, 1275 m, 24 Aug. 1993, *Fishbein et al. 1448* (ARIZ); ridge SW of Santa Barbara, 20 air mi. ENE of Alamos, 1450 m, 3 June 1993, *Jenkins 93-88* (ARIZ); Sierra de Alamos, ca. 900 m, 19 Aug. 1992, *Steinmann s.n.* (ARIZ); Palm Canyon, 17.7 mi. SE of Magdalena in Cerro Cinta de Plata, 2 Oct. 1976, *Van Devender et al. s.n.* (ARIZ); ca. 1200 m, *Van Devender & Eiber s.n.* (ARIZ), 16 July 1977, *Van Devender, Goldberg & Turner s.n.* (ARIZ). U.S.A. **New Mexico:** Hidalgo Co., Guadelupe Canyon, 16 Aug. 1979, *Spellenberg & Repass 5353* (NY).

9. Metastelma minutiflorum Wiggins, Contr. Dudley Herb. 3: 71. 1940. *Cynanchum sonorense* Moran, in Levin & Moran, Vasc. Fl. Isla Socorro, Mexico (Mem. San Diego Soc. Nat. Hist. 16): 26. 1989, non *C. minutiflorum* K. Schum., Nat. Pflanzenfam. 4(2): 252. 1895. TYPE: Mexico. Sonora: hills between Magdalena and Santa Ana, 7 mi. S of Magdalena, 14 Sep. 1934, *I. L. Wiggins 7191* (holotype, DS not seen; isotype, US!). Figures 10, 13a′–f′.

Plants ascending, to 150 cm high; *shoots* basally woody, with brownish bark, densely covered along two lines with recurved trichomes, 150–250 μm long; internodes 2.5–5 cm long, 1–1.5 mm diam. *Leaves* with petioles 5–6 mm long, with 1 or 2 colleters at blade base; blades (10–)20–50 × 3–5 mm, narrowly ovate or narrowly obovate, basally acute, apically acute, adaxially sparsely covered on the midrib and the margins with flexuous trichomes, 250–300 μm long, abaxially glabrous. *Inflorescences* always one per node, 3- to 6-flowered, all flowers open synchronously, sciadioidal, subsessile; *floral bracts* 0.4–0.5 × 0.2–0.3 mm at the base, triangular to ovate; *pedicels* 1–1.2 mm long, isolatedly covered over the entire surface with appressed trichomes, 140–200 μm long. *Floral buds* ca. 1.5 mm long, ca. 1 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially glandular, abaxially with sparse trichomes; calyx lobes 1–1.25 × 0.3–0.4 mm, ovate, apically acute; *corolla* campanulate, 1.7–2 mm long, abaxially cream, glabrous, adaxially white, with smooth trichomes, 150–250 μm long, on the apical and on the lateral parts of the lobes; lobes basally fused, 0.5–0.6 mm wide, patent to incurved, ovate, apically acute; *gynostegial corona* 0.6–0.7 mm long, shorter than to equaling the gynostegium; lobes erect, attached directly underneath the anthers, laminar, lanceolate. *Gynostegium* 0.7–0.9 mm high, 0.7–0.9 mm diam., subsessile; *anthers* about as high as broad, rectangular, abaxially planar; anther wings 0.4–0.5 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther; connective appendages 300–350 μm long, 200–250 μm wide, obcordate, equaling the stamen in width, slightly inflexed; *pollinarium* with corpusculum 75–80 μm long; caudicles 50 μm long, cylindrical, s-shaped, convex-concave, thickened at the insertion of the pollinium; pollinia apically attached to the caudicles, 75 μm long, 50 μm wide, ovate in cross section, reniform; *style-head* white, 0.3–0.4 mm diam., 0.4–0.5 mm high, upper part 1.5–1.7 mm high, shorter to equaling the lower part, conical to knobby. *Follicles* one per flower, 60–75 mm long, 4–5 mm diam., fusiform, terete, apically strongly beaked, blackish brown, glabrous; *seeds* 5–6 mm long, 3–3.5 mm wide, pyriform, seta and aseta side tuberculate, papillose with regularly arranged papillae, marginally wingless, denticulate; coma 15–20 mm long.

Phenology. Collected in flower in April, September, and November; in fruit in November.

Distribution. Mexico: Baja California, Sonora; thornscrub and grassland; 200–500 m.

Literature and illustrations. Wiggins (1940: 82, pl. 17).

Cynanchum minutiflorum is a name not available for this taxon, because it is preceded by *Cynanchum minutiflorum* K. Schum., Nat. Pflanzenfam. 4(2): 252. 1895, today considered a synonym of *C. schistoglossum* Schltr. (Liede, 1996b). Under *Metastelma*, however, *Metastelma minutiflorum* is available and thus valid. For comments on a close relationship, see *M. latifolium*.

Additional specimens examined. MEXICO. **Baja California Sur:** canyon of W slope of peak overlooking saltworks, Carmen Island, 4 Apr. 1962 (fl), *Moran 9141* (ARIZ). **Sonora:** near Piedras Verdes, N of Alamos, 2 Nov. 1939 (fl), *Gentry 4857* (NY, TEX); Yecora, 17 Sep. 1998 (fl), *Van Devender et al. 98-1285* (ARIZ).

10. Metastelma palmeri S. Watson, Proc. Amer. Acad. Arts 18: 115. 1883. *Cynanchum grayi* Shinners, Field & Lab. 20: 110. 1952. *Cynanchum maccartii* Shinners var. *maccartii*, Sida 1: 360. 1964, nom. nov. for *Cynanchum palmeri* (S. Watson) Shinners, Field & Lab. 19:

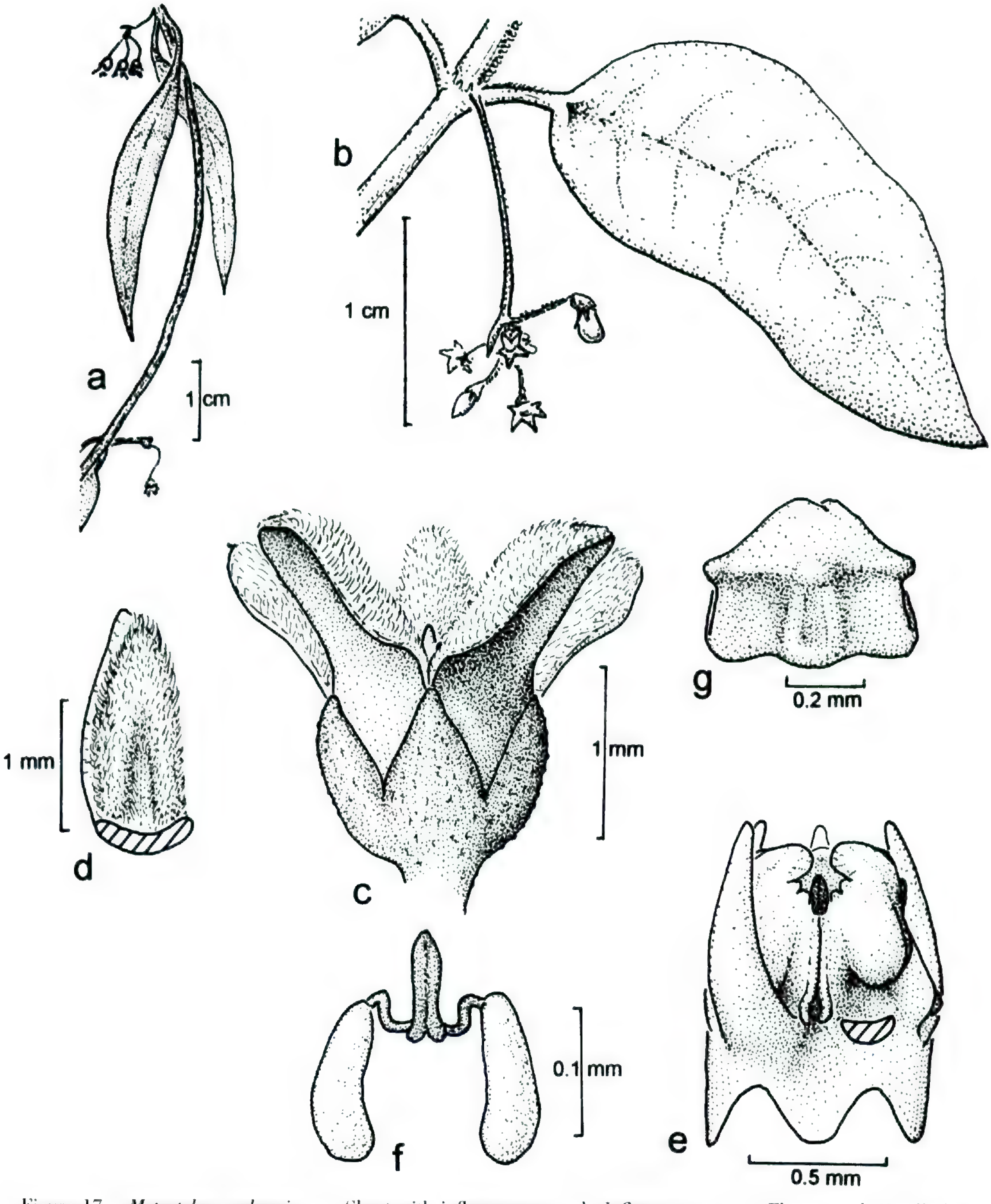


Figure 17. *Metastelma palmeri*. —a. Shoot with inflorescence. —b. Inflorescence. —c. Flower. —d. Corolla lobe, adaxial view. —e. Gynostegium and corona. —f. Pollinarium. —g. Style-head. a: *Palmer 828*. b: *Pringle 6706*. d–g: *Liede & Conrad 2612*. Drawn by J. Conrad.

65. 1951, non *Cynanchum palmeri* (S. Watson) Blake, Contr. Gray Herb. 52: 83. 1951. TYPE: U.S.A. Texas: Webb Co., Laredo on the Rio Grande, Aug. 1879, *E. Palmer 824* (lectotype, designated by Henrickson (1987: 98), GH not seen; isotype, NY!). Figure 17a–g.

Metastelma macropodum Greenm., Proc. Amer. Acad. Arts 33: 481. 1898. Syn. nov. TYPE: Mexico. Oaxaca: Tomellín Canyon, 1540 m, 17 July 1897, *C. G. Pringle 7606* (holotype, NY!; isotypes, HBG!, M!, MO not seen, P!, S!).

Plants ascending, 50–200(–400) cm high; *sub-*

terranean organs constituting a woody rootstock; *shoots* perennial, basally slightly woody, with yellowish brown to blackish bark, glabrous, isolatedly to sparsely covered along a single line with recurved to flexuous trichomes, 200–300 μm long; internodes 2–4 cm long, ca. 1 mm diam. *Leaves* with petioles 2–7 mm long, with 2 colleters at blade base; blades (12–)16–35(–55) × 2.5–7(–12) mm, ovate, basally rounded, apically acute, marginally revolute (when dry), adaxially isolatedly to sparsely covered, mainly or only on the midvein with appressed to recurved trichomes, 150–250 μm long, abaxially glabrous. *Inflorescences* always one per node, extra-axillary, 3- to 8-flowered, 2 to 6 flowers open synchronously, thyrsoidal to sciadioidal; *peduncles* 0–10 mm long, densely covered along a single line with recurved to flexuous trichomes, 150–200 μm long; *floral bracts* 0.4–0.7 × 0.2–0.5 mm at the base, triangular, glabrous; *pedicels* 0–5 mm long, glabrous or isolatedly to densely covered along a single line with recurved trichomes, 200–250 μm long. *Floral buds* 1.5–2 mm long, 0.8–1.5 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially glabrous or with a few sparse trichomes on the tube; lobes 0.5–1.3 × 0.2–0.5 mm, ovate, apically acute to obtuse; *corolla* campanulate, 2.2–3 mm long, abaxially white to cream, glabrous, adaxially white to cream, with smooth trichomes, 100(–150) μm long, on the apical and on the lateral parts of the lobes, apical trichomes not longer than lateral ones, and deflexed hispid trichomes on the central parts of the lobes; lobes basally fused, 0.6–1 mm wide, patent, ovate, apically acute, recurved; *gynostegial corona* 0.7–1 mm long, equaling to longer than the gynostegium; lobes erect to inflexed, attached directly underneath the anthers, laminar, ovate to triangular. *Gynostegium* 0.4–0.7 mm high, 0.5–0.8 mm diam., on a stipe 0.3–0.4 mm long; *anthers* about as high as broad, trapezoidal, abaxially planar; anther wings 200–250 μm long, extending along the entire length of the anther, the stamen forming a basal arch; anther wings of adjacent anthers parallel to each other, centrifugal, basally forming a distinct "mouth"; connective appendages 200–250 μm long, 250–300 μm wide, ovate, narrower than the stamen, slightly inflexed; *pollinarium* with corpusculum 100–150 μm long, between 1.5 times and twice as long as broad, ovoid to elliptic; caudicles 50–70 μm long, cylindrical, s-shaped, convex-concave; pollinia apically attached to the caudicles, 120–150 μm long, ca. 50 μm wide, ovate in cross section, oblongoid; *stylehead* white, 0.4–0.5 mm diam., 0.2–0.3 mm high, upper part 0.05–0.1 mm high, shorter than the lower part, depressed-conical to umbonate. *Follicles* one per flower, 40–60 mm long, 4.5–5.5 mm diam., fusiform, terete, apically strongly beaked, dark brown, glabrous; *seeds* 6–7 mm long, 3–4 mm wide, ovate, medium brown, seta and aseta side smooth, marginally with 0.1–0.2 mm wide wing with entire margin.

Phenology. Collected in flower from July to October; in fruit in August.

Distribution. Guatemala: Izabal; Mexico: Coahuila, Nuevo León, Oaxaca, Puebla, Tamaulipas, Yucatán; U.S.A.: Texas; on limestone, but also on igneous rock, matorral and thorn forest; 500–2000 m.

Literature and illustrations. Henrickson (1987: 98, fig. 1).

Apparently, the same author published two replacement names for *Cynanchum palmeri*, *Cynanchum grayi* (Shinners, 1952) and *Cynanchum maccartii* (Shinners, 1964). As there is no doubt about the intentions of Shinners (1952, 1964) in both cases, and *Cynanchum grayi* would have been a name available for the taxon, an error is the most probable cause for this duplication. Henrickson (1987) remedied the situation by designating the same lectotype for *M. palmeri* and *C. maccartii*.

Contreras 9336 from Guatemala and *Conrad 9319* from the Yucatán Peninsula, both out of the main distribution area in Mexico, display a corona a little more stout than usual, but are best accommodated here until more material from this area becomes available.

The specimens of *Metastelma macropoda*, a name applied to collections from central Mexico, are indistinguishable from those of *M. palmeri*, and *M. macropoda* is thus placed in synonymy of *M. palmeri*.

The flowers in the *Metastelma palmeri* complex are easily confused with those of *M. minutiflorum* and *M. latiflorum*, which show a very similar structure. However, *M. latifolium* and *M. minutiflorum* occur along the Pacific slope, while *M. palmeri* occurs along the Gulf Coast. Morphologically, *M. palmeri* can be distinguished by slightly larger flowers (corolla 2–3 mm long on average in contrast to less than 2 mm in *M. latifolium* and *M. minutiflorum*), broader and longer corona lobes (basally as broad as the anthers, and as long as or slightly longer than the gynostegium in contrast to smaller than the anthers throughout and never exceeding the gynostegium in *M. latifolium* and *M. minutiflorum*), and a more clearly stipitate gynostegium. Most conspicuous, though only visible under a dissecting microscope, are the very tiny pollinaria (120–150 × ca. 50 μm) with their thin and fragile caudicles.

Additional specimens examined. GUATEMALA. **Iza-**

bal: Cadenas (Puerto Mendez), 13 Oct. 1969 (fl), *Contreras 9336* (LL, NY). MEXICO. **Coahuila:** Canyon la Gavia, in N side of Sierra de la Gavia, 2 Aug. 1973 (fl, fr), *Henrickson 11724* (TEX); Catacol Mts., Aug. 1880 (fl), *Palmer 828* (NY); 22 km ESE of La Cuesta del Plomo on the Múzquiz–Boquillas Hwy., 7 June 1972 (fl), *Chiang et al. 7550* (NY, TEX); Hacienda Mariposa, at the foot of the eastern slope of the Sierra de Puerto Santa Ana, 23 June 1936 (fl), *Wynd & Mueller 244* (ARIZ, NY, WIS); Múzquiz, Palm Canyon, 7 Sep. 1936 (fl), *Marsh 305* (TEX); Rancho Las Tres Sabinas ca. 15 km W of Músquiz, 5 June 1972 (fl), *Chiang et al. 7527A* (TEX); Rincón de Maria, 24 Aug. 1975 (fl), *Wendt et al. 1328* (TEX); Hwy. 57, 70 mi. N of Saltillo, 3 June 1966 (fl), *Wilson 11388* (TEX). **Nuevo León:** Mts. W of Bustamante, Aug. 1938 (fl), *LeSueur 361* (TEX); Old Pass road, Paso de Mamulique, 8 Aug. 1989 (fl), *Liede & Conrad 2612* (UBT). **Oaxaca:** Concepción Buenavista, base del Cerro Pluma, Santa Lucia, 4 July 1994 (fl), *Panero & Calzada 4026* (LL); distr. Huajuapan, 15 km al o de Tamazulapan, 13 July 1986 (fl), *Mendoza & Mérida 2566* (LL); La Reforma entre Huajuapan de León y Tamazulapan, 6 June 1985 (fl), *Torres & Garcia 6656* (LL). **Puebla:** Agua Los Granados, ca. 20 km al O de Axusco, 24 Sep. 1990 (fl), *Salinas 5790* (NY); near Oaxaca, cerro de Costapa near San Luis Tultitlanapa, June 1908 (fl), *Purpus 3244* (NY). **Tamaulipas:** 4.4 mi. NE of turnoff to Bustamante on Hwy. 101 15 June 1987 (fl), *Nesom et al. 5957* (LL); Carretera Victoria–San Luis Potosí, 8 mi. S of Palmillas, 20 July 1985 (fl), *Ginzbarg 131* (TEX); along Hwy. 85, about 8.6 mi. N over river bridge at Colonia Mirador, 30 June 1976 (fl), *Stevens et al. 2260* (NY); 37 mi. out of Reynosa on the rd. to San Fernando, 19 Oct. 1959 (fl), *Johnston 4369* (TEX); near microwave tower above Villagran, 30 June 1976 (fl), *Stevens et al. 2259* (NY). **Yucatán:** Celestún Nat. Park, ca. 5 km N Celestún, 16 May 1993, *Conrad 9319* (UBT). U.S.A. **Texas:** Brewster Co., end of trail down from Mt. Emory to camp in Basin, 2 Sep. 1947 (fl), *Hinckley 4088* (NY); Jefferson Davis Co., Point of Rock on Ft. Davis–Valentine Hwy., 27 July 1947 (fl), *Hinckley 3954* (NY); Live Oak Co., road to Fiesta Marina just E of Rte. 534, 4.6 mi. N of Rte. 359, 26 July 1981 (fl), *Hill 10627* (NY).

11. Metastelma pedunculare Decne., in A. P. de Candolle, Prodr. 8: 514. 1844. *Cynanchum woodsonianum* L. O. Williams, Fieldiana, Bot. 32: 42. 1968, non *Cynanchum pedunculare* Lam. 1786. TYPE: Guatemala. Cuesta de Piñula, 1837, *K. T. Hartweg 601* (holotype, G not seen; isotypes, NY—2!, P!). Figures 12, 18a–f.

Metastelma sepicola Pittier, Contr. U.S. Natl. Herb. 13: 98. 1910. *Cynanchum sepicola* (Pittier) L. O. Williams, Fieldiana, Bot. 32: 40. 1968. TYPE: Costa Rica. San José: July 1896, *A. Tonduz s.n.* (holotype, US!; isotype, P!).

Plants ascending; *shoots* perennial, basally woody, with grayish bark, glabrous. *Leaves* with petioles 4–7 mm long, with 0 to 2 colleters at blade base; blades 25–60 × 7–17 mm, ovate, basally rounded, apically acute to acuminate, adaxially glabrous or sparsely covered only on the midvein with recurved trichomes, 300–400 μm long, abaxially glabrous. *Inflorescences* always one per node, 6- to 8-flowered, one specimen more than 15- to 20-flowered (*Molina 23080*), 1 to 3 flowers open synchronously, bostrychoid; *peduncles* 10–25 mm long, densely covered along a single line with recurved trichomes, 100–150 μm long; rachis 0–2 mm long, straight or 3–17 mm long, angular (*Molina 23080*); *floral bracts* 0.3–0.4 × ca. 0.2 mm at the base, triangular, ciliate; *pedicels* 3–5 mm long, glabrous. *Floral buds* 1.5–2.5 mm long, 1–1.5 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially glabrous, ciliate or with very few trichomes; calyx lobes ca. 0.6 × ca. 0.3 mm, ovate, apically acute; *corolla* campanulate, 2–3.5 mm long, abaxially cream, glabrous, adaxially creamish white, with verrucose trichomes, 100–150 μm long, on the lateral parts of the lobes; lobes fused for ca. ⅓ of total corolla length, ca. 0.7 mm wide, horizontal to recurved, ovate, apically acute; *gynostegial corona* 0.5–0.6 mm long, equaling the gynostegium; lobes inflexed, attached directly underneath the anthers, laminar, oblong. *Gynostegium* 0.3–0.5 mm high, 0.6–1 mm diam., on a column 0.6–1 mm long or only 0.3 mm long (*Molina 23080*); *anthers* broader than high, rectangular, abaxially planar; anther wings 200–250 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther; connective appendages ca. 250 μm long, ca. 250 μm wide, ovate, narrower than the stamen, strongly inflexed; *pollinarium* with corpusculum ca. 200 μm long, more than twice as long as broad, elliptic; caudicles ca. 150 μm long, cylindrical, s-shaped, convex-concave; pollinia ca. 200 μm long, ca. 75 μm wide, ovate in cross section, clavate; *style-head* white, 0.6–1 mm diam., 0.2–0.3 mm high, upper part flat. *Follicles* and *seeds* not seen, follicles 45 mm long (fide Standley, 1938).

Phenology. Collected in flower in July, August, and November.

Distribution. Costa Rica: Cartago, San José; Guatemala: Guatemala; Nicaragua: Estelí; volcanic soil, in ravines, thickets, along borders of fields; 1000–1800 m.

Literature and illustrations. Pittier (1910: 97, fig. 5).

Specimens from Guatemala and Costa Rica show no constant differing characters, as Standley (1938b) observed correctly. He (Standley, 1938b) placed *Metastelma sepicola* in synonymy of *M. pedunculare*.

In *Metastelma pedunculare* an exceptionally long and slender column (to 1 mm) carries the short and

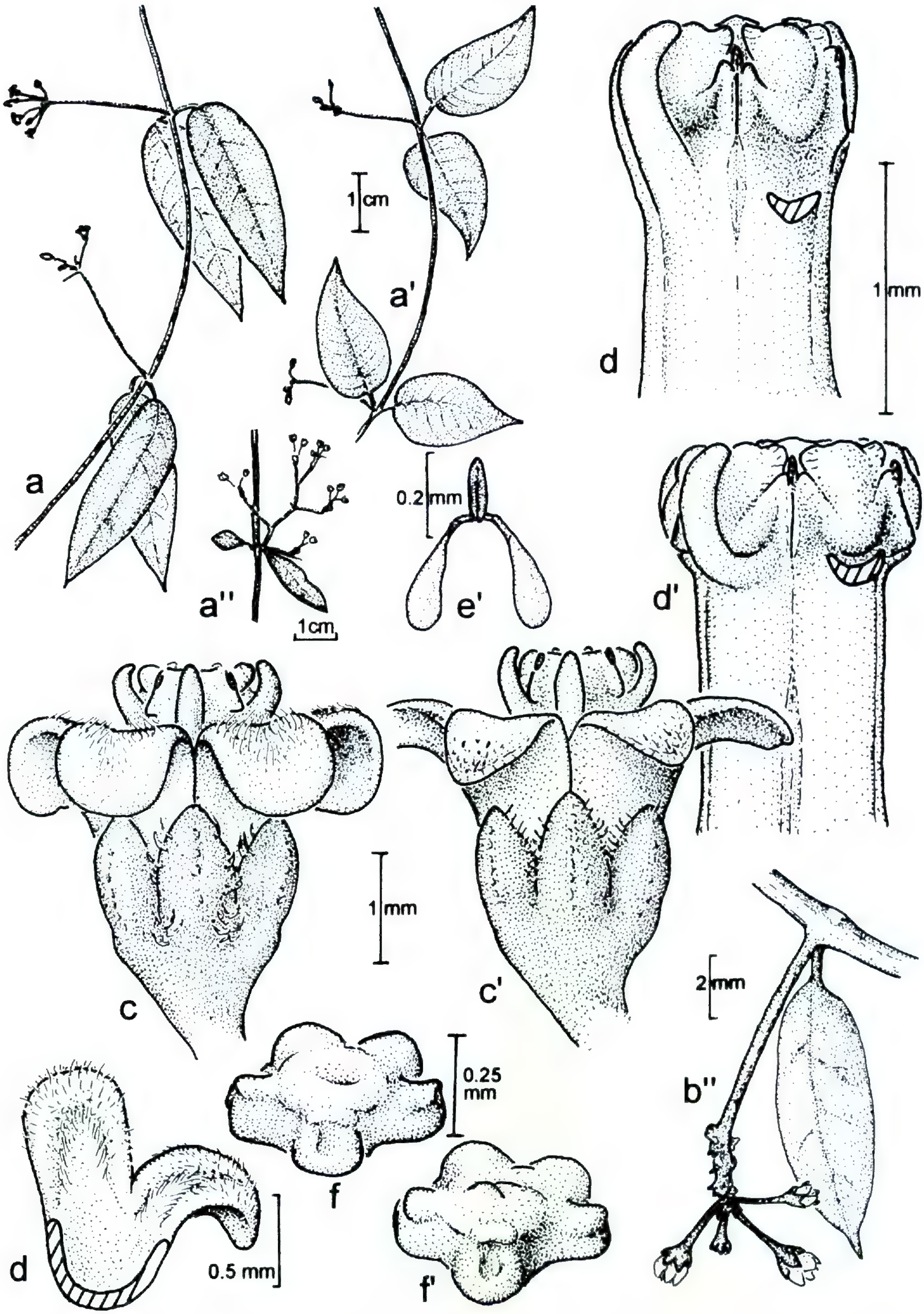


Figure 18. *Metastelma pedunculare*. —a, a', a''. Shoot with inflorescence. —b''. Inflorescence. —c, c'. Flower. —d. Corolla lobes, adaxial view. —d, d'. Gynostegium and corona. —e'. Pollinarium. —f, f'. Style-head. a–f: Specimens from Guatemala. a: *Hartweg 601*. c–f: *Molina & Molina 24843*. a'–f': Specimens from Costa Rica. a': *Tonduz s.n.* b'–f': *Taylor & Taylor 11393*. a'', b'': Specimen from Nicaragua, *Molina 23080*. Drawn by J. Conrad.

flat gynostegium. The short laminar corona lobes are inserted directly beneath the anthers and are curved along the back of the anthers in a hook-like manner. In *M. stenomeres*, the only other highly stipitate species with the corona lobes inserted directly underneath the gynostegium, the corona lobes are much longer than the gynostegium, while they barely exceed it in *M. pedunculare*.

Molina 23080 from Nicaragua, a specimen cited by Stevens (2001) as representative of *Metastelma* species "B," is easily identified by its bostrychoid inflorescences, which are, however, more richly branched than in other specimens. Also, compared to material from Guatemala and Costa Rica, the stipe and the corolla tube are quite short. However, gynostegium and corona structure agree well with *M. pedunculare*, so *Molina 23080* is included here until more material becomes available from which it can be judged whether the characters described for *Molina 23080* are typical for Nicaraguan material and can be used to circumscribe a subspecies of *M. pedunculare*.

Additional specimens examined. COSTA RICA. **Cartago:** 3 km SE of Cartago, 11 Aug. 1967 (fl), *Taylor 4251* (NY), *4285* (NY). **Puntarenas:** Rio Guacimal valley, 6 Oct. 1984 (fl), *Haber 615* (LL, WIS). **San José:** about 1 km NW of San Juan de Tibas along the Rio Virillo, 1 Aug. 1972 (fl), *Taylor & Taylor 11393* (NY); entre Frailes y La Sierra, 26 Nov. 1964 (fl), *Jímenez 2617* (NY); Acosta, *Endress 97-18* (UBT). GUATEMALA. **Guatemala:** 7 km E of Guatemala City, 24 Aug. 1970 (fl), *Harmon 4189* (NY); betw. km 18 to 22 on Hwy. from Guatemala City to Antigua, 26 Nov. 1969 (fl), *Molina & Molina 24843* (NY). NICARAGUA. **Estelí:** along Estanzuela Creek, 8 km W of Estelí, 4 Nov. 1968 (fl), *Molina 23080* (NY).

12. Metastelma pringlei A. Gray, Proc. Amer. Acad. Arts 21: 396. 1886. *Cynanchum pringlei* (A. Gray) Henr., Sida, 12: 91. 1987. TYPE: Mexico. Chihuahua: near Chihuahua, 23 May 1885, *C. G. Pringle 62* (holotype, GH not seen; isotype, US!). Figures 19a–f, 20.

Cynanchum barbigerum (Scheele) Shinners var. *breviflorum* Shinners, Sida 1: 360. 1964. TYPE: U.S.A. Texas: Brewster Co., Big Bend National Park, Chisos Mtns., 1800 m, 19 July 1952, *G. L. Webster 4340* (holotype, SMU not seen).

Plants ascending to decumbent, 100–400 cm high; *subterranean organs* constituting a woody rootstock (*Hinckley 2105, 3106*); *shoots* perennial, basally slightly woody, with yellowish brown or grayish bark, rarely glabrous, normally sparsely covered along a single thin line with recurved trichomes, 150–250 μm long; internodes 1–4 cm long, 1 mm diam. (green shoots) or 2–3 mm diam. (woody parts). *Leaves* with petioles 2–5 mm long, with 1 or 2 colleters at blade base; blades 10–20(–30) × 2–10 mm, ovate to elliptic, basally rounded, apically acute, marginally revolute (when dried), adaxially glabrous (except for a few isolated trichomes on midvein and the margin), abaxially glabrous. *Inflorescences* 2- to 6(to 12)-flowered, 2 to 6 flowers open synchronously, sciadioidal; *peduncles* 0–2 mm long, densely covered along a single thick line with recurved trichomes, 150–250 μm long; *floral bracts* 0.6–1.2 × 0.3–0.6 mm at the base, triangular, glabrous; *pedicels* 1.2–2.5(–4) mm long, glabrous, sparsely covered along a single line with recurved trichomes, ca. 200 μm long. *Floral buds* 2.3–3 mm long, ca. 1.5 mm diam., ovoid; *calyx* basally fused, abaxially glabrous; calyx lobes 1–1.2 × 0.4–0.5 mm, ovate, apically acute; *corolla* campanulate, 2.8–4 mm long, abaxially white or yellow to brown (when dry), glabrous, adaxially white, with slightly verrucose trichomes, 200–700 μm long, on the lateral and apical parts of the lobes, apically very long and wavy, and with hispid retrorse hairs, 300–500 μm long, on the central parts of the lobes; lobes fused for ca. ⅓ of total corolla length, 0.7–1.2 mm wide, patent, oblong to lanceolate, apically thickened, acute, with straight thickened margins; *gynostegial corona* 1.3–1.8 mm long, twice as long as the gynostegium; lobes erect, attached at the base of the stipe, solid to filiform, subulate, extended into a long, slender tip, often incurled or coiled. *Gynostegium* 0.5–0.7 mm high, ca. 0.7 mm diam., on a stipe 0.5–0.7 mm long; *anthers* broader than high, trapezoidal, abaxially planar; anther wings ca. 250 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, centrifugal; connective appendages 200–300 μm long, 200–300 μm wide, ovate, narrower than the stamen, slightly inflexed; *pollinarium* with corpusculum ca. 180 μm long, more than twice as long as broad, elliptic; caudicles ca. 50 μm long, cylindrical, geniculate, thickened at the insertion of the pollinium; pollinia apically attached to the caudicles, ca. 200 μm long, ca. 80 μm wide, ovate in cross section, ovoid; *style-head* white to cream, ca. 0.6 mm diam., ca. 0.5 mm high, upper part ca. 1.6 mm high, shorter than the lower part, depressed-conical. *Follicles* one per flower, 40–62 mm long, ca. 5 mm diam., obclavate to fusiform, terete, apically strongly beaked, dark brown, glabrous; *seeds* 5–6 mm long, 2.5–3 mm wide, ovate, reddish light brown, seta and aseta side smooth, marginally with 3 mm wide wing with entire margin; coma 20–25 mm long.

Phenology. Collected in flower from May to October; in fruit in April, and from June to October.

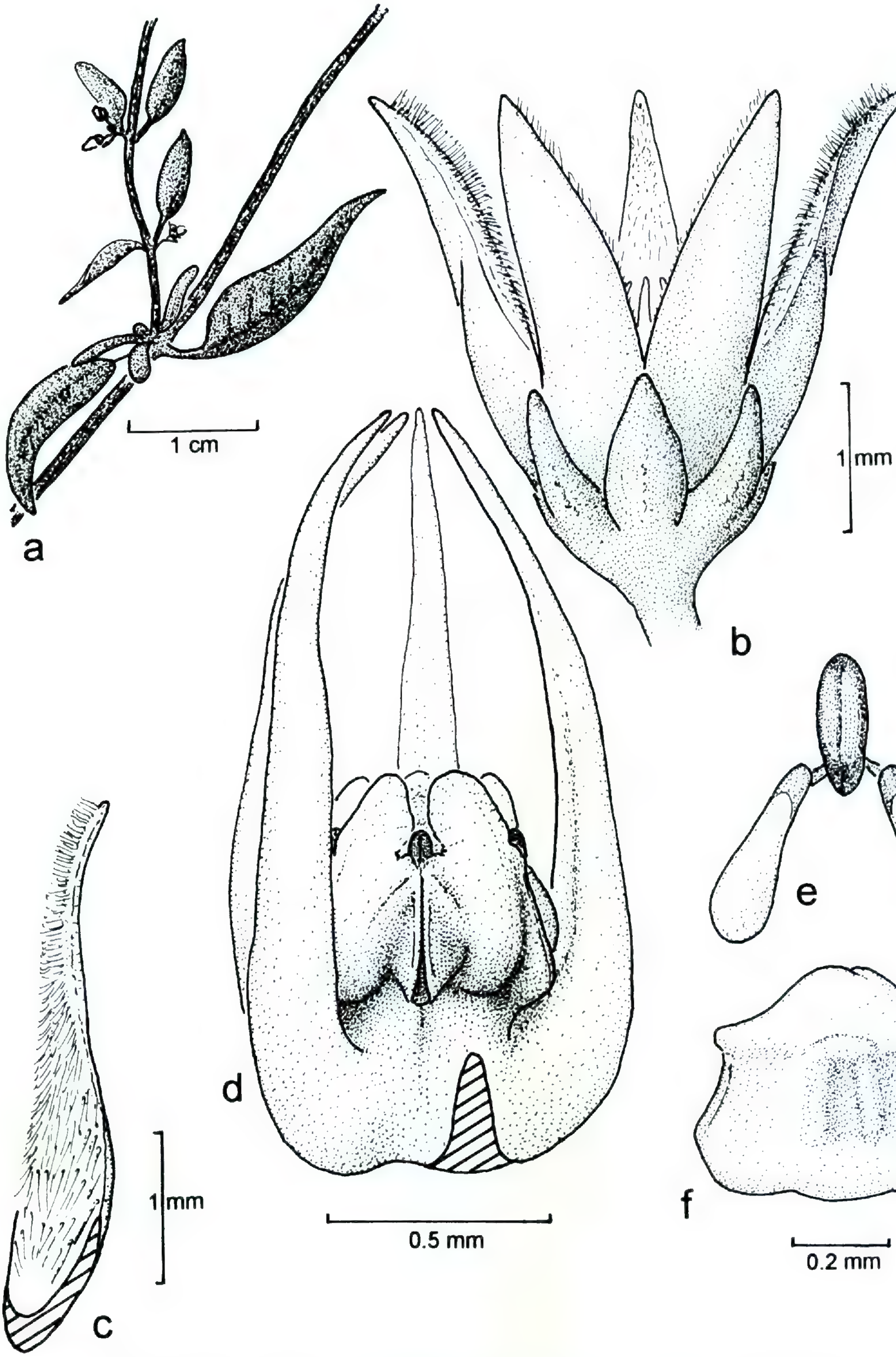


Figure 19. *Metastelma pringlei*. —a. Shoot with inflorescences. —b. Flower. —c. Corolla lobe, adaxial view. —d. Gynostegium and corona. —e. Pollinarium. —f. Style-head. a–f: *Pringle 62*. Drawn by J. Conrad.

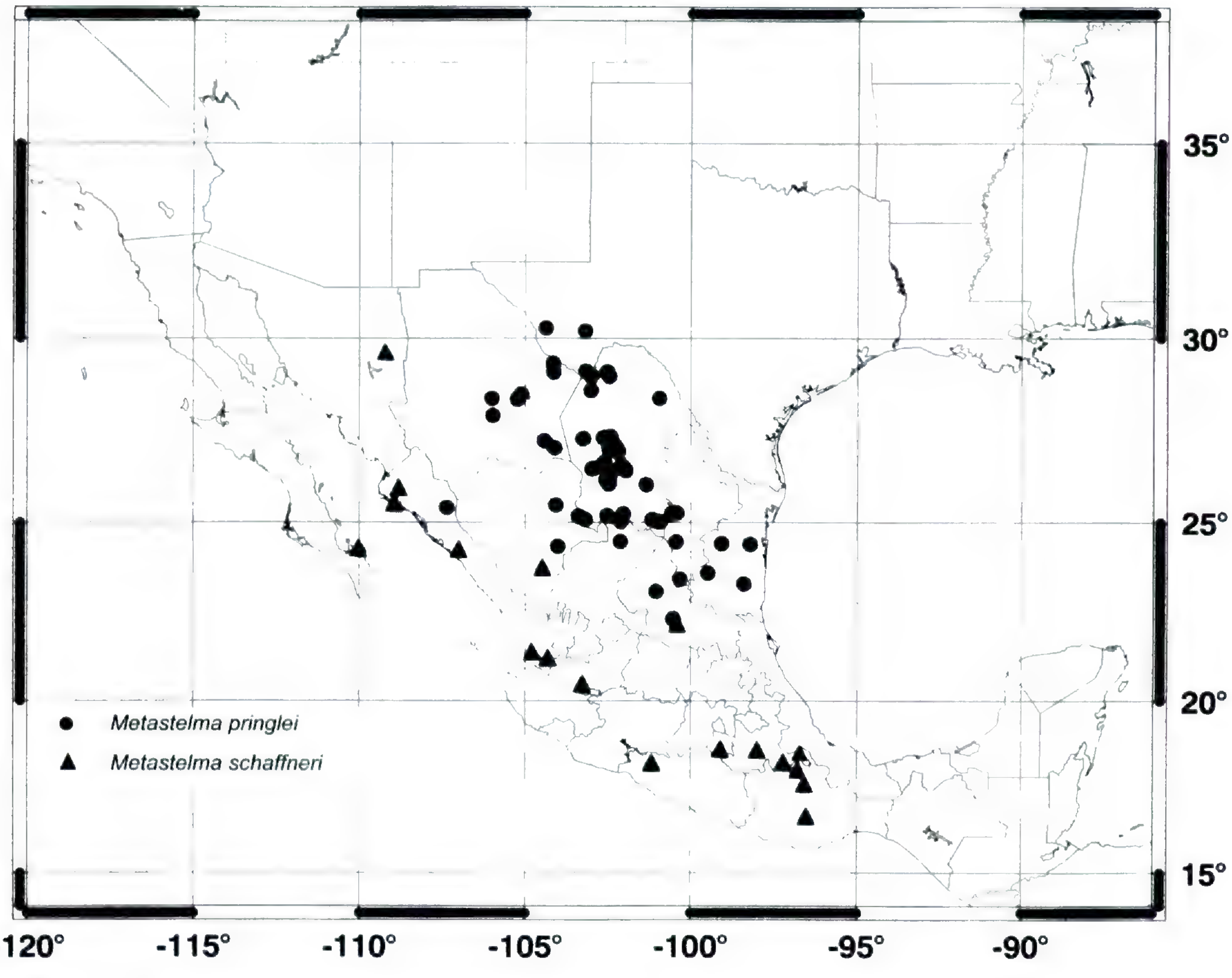


Figure 20. Distribution of *Metastelma pringlei* and *M. schaffneri*.

Distribution. Mexico: Chihuahua, Coahuila, Durango, Nuevo León, San Luis Potosí, Tamaulipas, Zacatecas; U.S.A.: Texas; rocky slopes, limestone, gypsum and lava, matorral, open pine forest, scrub, roadsides; 500–2300 m.

Literature and illustrations. Wiggins (1940: 82); Henrickson (1987: 93, fig. 1c–e).

The impressive crown formed by the long (to 1.8 mm), erect and often incurled corona lobes makes *Metastelma pringlei* an easily recognized species. The corolla indumentum with two different types of hairs, the conical gynostegium and the caudicles, which are apically inserted to the conical pollinia via a thickened, convex area, demonstrate its close relationship to *M. barbigerum* (cf. Fig. 1a, b). Shinners (1964) even described U.S. material of *M. pringlei* as a variety under *M. barbigerum*. However, the two species are easily and consistently separable by the corona lobes ca. twice as long as the gynostegium in *M. pringlei* (less than 1.5 times as long in *M. barbigerum*). Only one specimen has been found that is possibly a hybrid between the two species (Mexico. Coahuila: 13 mi. S of Sabinas, 23 Aug. 1938, *Shreve 8417*, ARIZ). It displays the slender leaves of *M. pringlei* in combination with a corona a little longer, but not twice as as long as the gynostegium and the bearded corolla lobes typical for *M. barbigerum* subsp. *barbigerum*.

Additional specimens examined. MEXICO. **Chihuahua:** 4 km SSW of Cerro del Gringo in the Sierra del Diabolo, 30 Aug. 1972, *Chiang et al. 9015f* (TEX); hills near Chihuahua, 5 Sep. 1886, *Pringle 955* (NY); Mts. NW of Chihuahua, 1 Aug. 1936, *LeSueur 1053* (TEX); Santa Eulalia Mts., 1885, *Pringle 70* (NY, UPS); Sierra de la Campana, Rancho La Campana, 5 June 1977, *Socorro Gonzales 840* (TEX); S slope & top of Sierra del Roque, NNE of Julimes, 19 June 1973, *Chiang et al. 11387* (TEX); ca. 31 (air) mi. NE of Julimes, SW facing canyon above Rancho el Recuerdo in Sierra de Carrasco, 15 Sep. 1973, *Henrickson 12980b* (TEX). **Coahuila:** Arroyo Seco, en el rancho el Tunal entre las Sierras San José y El Tunal, al E de Parras de la Fuente, 14 Aug. 1983 (fl), *Andréz Rodriguez & Carranza 1111* (ARIZ, LL); ca. 12 (air) mi. E of Boquillas in Sierra del Carmen, 10.4 (rd.) mi. NW of Rancho El Jardin, 27 July 1973 (fl), *Henrickson 11497* (LL); Cañon San Lorenzo, SE of Saltillo, 2 Aug. 1975 (fl), *Engard & Gentry 686* (LL); Canyon de Tinaja Blanca, central mass of Sierra de las Curces W of Santa Elena Mines, 14 Aug. 1940 (fl), *Johnston & Muller 261* (TEX); ca. 6.9 mi. SW of Cuatro Ciénegas on Hwy. to San Pedro, 27 Sep. 1986 (fl, fr), *Henrickson 20400* (LL); 8 km W of Cuatro

Ciénagas, slopes of Sierra de la Madera, 5 Aug. 1973 (fl), *Johnston et al. 12077* (NY, TEX); ca. 35 (air) mi. W of Cuatro Ciénegas, in mid-Canyon de la Hacienda of Sierra de la Madera, 6 Aug. 1973 (fl), *Henrickson & Wendt 12028* (LL); ca. 43 (air) mi. W of Cuatro Ciénegas, 4 mi. SW of Hacienda Zacatosa, 7 Aug. 1973 (fl), *Henrickson 12070* (LL); 52 mi. WNW of Cuatro Ciénegas (12 mi. E of La Vibora), 20 Sep. 1972, *Henrickson 7891* (LL); ca. 67 (air) mi. SW of Cuatro Ciénegas, above the main spring, 1.5 mi. SW of Las Delicias, 15 Aug. 1973 (fl, fr), *Henrickson 12481* (LL); ca. 23 (air) mi. NW of Las Delicias, valley N of Sierra de las Delicias near old mine, 29 Aug. 1971 (fl), *Henrickson 6100* (LL); 16 km by winding road almost due N of Ejido Piedritas, 17 Sep. 1972 (fl, fr), *Chiang et al. 9366a* (NY); rd. from Esmeralda NE to San Antonio de los Alamos (via Bufido and Empleado), 1 Sep. 1940 (fl), *Johnston & Muller 834* (LL); 4 km E of Fraile, 12 July 1941 (fl), *Stanford et al. 362* (ARIZ, NY); E of Hacienda La Rosa, 14 June 1936 (fl), *Wynd & Mueller 26* (ARIZ, NY); 11 km NE of Jimulco, 28 June 1941 (fl), *Stanford et al. 68* (NY); 12.6 km NNE of Las Margaritas in a large canyon E face of Sierra de las Margaritas, 21 Sep. 1972 (fl), *Chiang et al. 9501* (LL); at La Morada Ranch, 28 Aug. 1968 (fl), *McKellar s.n.* (LL); S of Parras, 19 Sep. 1993 (fl), *Hinton 23343* (TEX); W base of Picacho del Fuste, NE from Tanque Vaionetta, 23 Aug. 1941 (fl), *Johnston 8438* (LL); Porción W de la sierra la Madera, ca. 45 km rumbo a Sierra Mojada, 10 Sep. 1991 (fl, fr), *Carranza & García 1080* (TEX); 2.5 mi. S of Poso de la Becerra along Cuatro Ciénegas Hwy. S, 5 Apr. 1969 (fl, fr), *LaBounty et al. 5947* (LL); Puerto de Ventanillas, 14 Aug. 1978 (fl, fr), *Burgess & Van Devender 5235* (ARIZ); SW flank of Sierra del Carmen, 15 Sep. 1972 (fl), *Chiang et al. 9274* (LL); 1.5 mi. S of Rte. 40 on road to canyon, 5 mi. E of Jct. with Ramos Arizpe rd. and Rte. 40, 15 Aug. 1979 (fl), *Wagner et al. 4120* (LL); vicinity of Rancho El Tule, ca. 24 km due N of Castillon & close to the Chihuahuan boundary, 13 June 1941 (fl), *Stewart 466* (LL); Rancho Los Angeles, 54 km S de Saltillo, 28 July 1982 (fl), *Vilaseñor et al. 1621* (LL); N end of Sierra de la Fragua, E of Estacion Belloc, 38 km W of Cuatro Ciénegas, 19 Oct. 1985 (fl), *Lavin et al. s.n.* (LL); Sierra de San Antonio, canyon at San Antonio de los Alamos, 2 Sep. 1940 (fl), *Johnston & Muller 950* (LL); Sierra de Parras, ca. 18 km S de Parras de la Fuente, 14 Oct. 1983 (fl, fr), *Rodríguez 1024* (ARIZ); Sierra San Marcos, W of Reynolds Mine Headquarters, Casa Colorado turnoff W of San Lazaro Pass, Hwy. 57, 12 July 1974 (fl), *Engard & Getz 331* (ARIZ, LL); N end of Sierra San Marcos, S of Cuatro Cienagas, 9 May 1973 (fl), *Gentry & Engard 23247* (ARIZ); lower canyon & bajada of Sierra San Marcos opposite Laguna Grande, 14 Aug. 1975 (fl), *Reeves & Pinkava 13075* (NY); S part of Sierra de los Organos, ca. 9.5 km E of Puerto del Gallo, 8 Aug. 1973 (fl), *Johnston et al. 12125B* (LL). **Durango:** ca. 1 km WSW of Luis Moya at Estacíon Microondas Las Campanas, 23 June 1973 (fl), *Johnston et al. 11457A* (TEX); 26 mi. W of Mapimi, Rte. 30, 26 July 1958 (fl), *Correll & Johnston 20219* (LL); ca. 26 (air) mi. SW of Torreon, 6.8 (rd.) mi. NW of Hwy. 40 toward Presa Francisco Zarca, 11 Aug. 1976 (fl), *Henrickson & Prigge 15352* (LL). **Nuevo León:** ca. 15 mi. N of Matehuela along Hwy. 57, 24 July 1977 (fl, fr), *Bennett et al. 646* (MO, NY, TEX); La Becerra, 5 Sep. 1989 (fl), *Hinton et al. 19616* (LL); El Barrial, 4 Sep. 1979 (fl), *Hinton 17660* (LL); La Soledad, 26 Aug. 1940 (fl, fr), *Shreve & Tinkham 9694* (ARIZ); Hacienda Pablillo, Galeana, 14 Aug. 1936 (fl), *Taylor 172* (ARIZ, LL). **San Luis Potosí:** 6.5 (rd.) mi. S of Arista, in Chihuahuan Desert, 6 Sep. 1971 (fl, fr), *Henrickson 6427* (TEX); Ejido Cerrito Blanco, 10 km al E de Matehuala, 6 Oct. 1980 (fl), *Iemus 11* (WIS); Charcas, July–Aug. 1934 (fl), *Lundell 5517* (WIS). **Tamaulipas:** ca. 46 km WNW of Jaumave; 6.5 rd. km W of Miquihuana, 8 Oct. 1982 (fl), *Henrickson 19138b* (TEX); 5 km al N de Estanque de los Valles o 25 km al NW de Miquihuana, 4 June 1986 (fl), *Hernandez 1917* (TEX). **Zacatecas:** 12.5 (rd.) mi. NNE of Rancho Hidalgo, ca. 27 mi. NNW of Camacho, in Chihuahuan Desert, 2 Sep. 1971 (fl, fr), *Henrickson 6366b* (LL). U.S.A. **Texas:** Brewster Co., Blue Creek Canyon, Old Wildon Ranch, Big Bend Nat. Park, 23 Sep. 1966 (fl), *Correll 33825* (NY); W side of Old Blue, Glass Mts., 2 June 1941, *Warnock 21851* (NY); Big Bend, Window Trail, 7 Mar. 1989 (fl, fr), *Liede & Meve 2501* (MO); Chisos Mts., 22 June 1931 (fl), *Müller 8115* (NY). Presidio Co., ca. 1 mi. S of Vieja, 14 Aug. 1941 (fl), *Hinckley 2105* (NY); S side of Chinati, W of Shafter, 14 Aug. 1941 (fl, fr), *Hinckley 3106* (NY). County not known: Valley of the Rio Grande, below Doñana, *Emory 1057* (NY).

13. Metastelma schaffneri A. Gray, Proc. Amer. Acad. Arts 21: 396. 1886. TYPE: Mexico. San Luis Potosí: near San Luis Potosí, 1876, *J. G. Schaffner 652* (holotype, GH!; isotype (fragment), NY!). Figures 20, 21a–g.

Metastelma multiflorum S. Watson, Proc. Amer. Acad. Arts 25: 158. 1890. Syn. nov. TYPE: Mexico. Jalisco: Guadalajara, 5 Nov. 1888, *C. G. Pringle 1776* (lectotype, designated here, NY 00279057!; isotypes, F not seen, neg. 051460, GH not seen, M!, NY!, P!, S!, UPS!).

Plants ascending, to 200 cm high; *shoots* perennial, glabrous, sparsely covered along a single line with flexuous trichomes; internodes 25–30 cm long. *Leaves* with petioles 1–2 mm long, with 2 colleters at blade base; blades 15–25 × 1.5–12 mm, linear to elliptic to ovate, basally rounded, apically acute to acuminate, marginally revolute (when dry), adaxially sparsely, abaxially isolatedly covered only on the midrib and the margins with recurved trichomes, 180–200 μm long. *Inflorescences* 4- to 6-flowered, 2 to 5 flowers open synchronously, sciadioidal, subsessile; *floral bracts* 0.6–1.2 × 0.3–0.4 mm at the base, triangular, glabrous or with trichomes on the surface; *pedicels* 1–3 mm long, glabrous. *Floral buds* 2–2.5 mm long, 1–1.3 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially glabrous or with trichomes, mainly on the tube; calyx lobes 0.8–1.2 × 0.3–0.5 mm, ovate to triangular, apically strongly acute; *corolla* campanulate, 2–3 mm long, abaxially white with purple, glabrous, adaxially white, smooth trichomes, 150–180 μm long, on the lateral and on the apical parts of the lobes; lobes fused to ca. ⅓ of total corolla length, 0.7–0.8 mm wide, patent, ovate, apically acute; *gynostegial corona* 0.6–0.8 mm long, longer than the gynostegium; lobes erect, attached directly

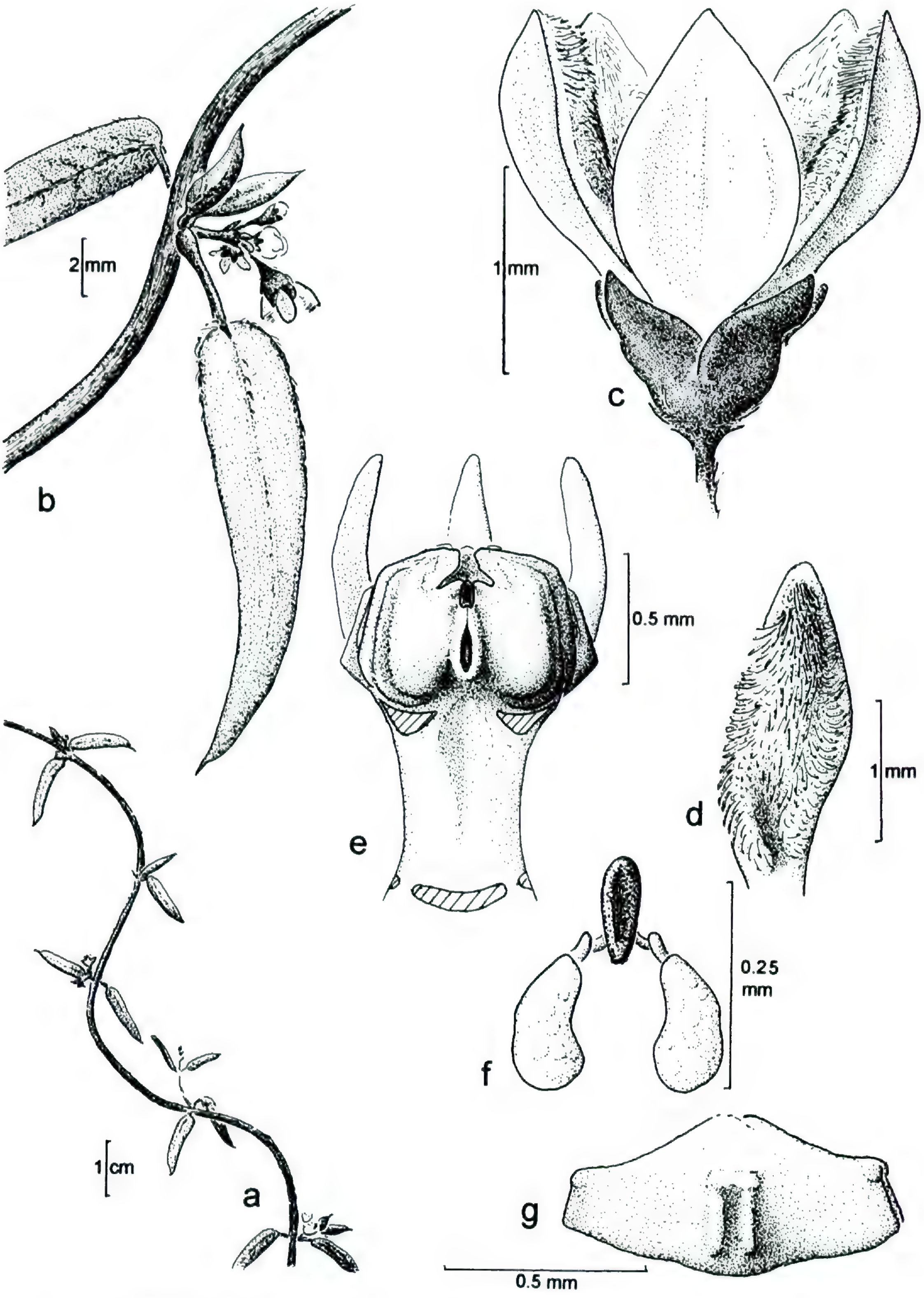


Figure 21. *Metastelma schaffneri.* —a. Habit. —b. Shoot with inflorescences. —c. Flower. —d. Corolla lobe, adaxial view. —e. Gynostegium and corona. —f. Pollinarium. —g. Style-head. a–g. *Pringle 1776.* Drawn by J. Conrad.

underneath the anthers, laminar, ovate. *Gynostegium* 0.5–0.6 mm high, 1–1.2 mm diam., on a column 0.3–0.4 mm long; *anthers* broader than high, rectangular, abaxially planar; anther wings ca. 400 μm long, anther wings of adjacent anthers parallel to each other, basally widened, in the same plane as the anther; connective appendages 250–300 μm long, 350–400 μm wide, ovate, narrower than the stamen, slightly inflexed; *pollinarium* with corpusculum 100–150 μm long, more than twice as long as broad; caudicles 70–100 μm long, cylindrical, slightly s-shaped, convex-concave; pollinia apically attached to the caudicles, 150–200 μm long, 80–100 μm wide, ovate in cross section, reniform; *style-head* green, 0.8–0.9 mm diam., 0.4–0.5 mm high, upper part 0.1–0.2 mm high, shorter than the lower part, depressed-conical. *Follicles* ca. 55 mm long, ca. 5 mm diam., obclavate, terete, apically strongly beaked, medium brown, glabrous; *seeds* ca. 15 per follicle, 6–6.5 mm long, 3 mm wide, ovate, seta and aseta side smooth, marginally with ca. 0.5 mm wide wing with entire margin.

Phenology. Collected in flower in June, and from August to March; in fruit March, August, and September.

Distribution. Mexico: Baja California, Durango, Guerrero, Jalisco, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa, Sonora; hillsides and ravines, savanna, low open deciduous forest; 500–2900 m.

Lectotypification of *Metastelma multiflorum* is necessary because there is no clue in the protologue as to where a holotype specimen was deposited. Of the many isotype specimens distributed, the NY 00279057 specimen is selected because it is accompanied by a nice drawing.

Of the small-flowered *Metastelma* species with dense indumentum on the adaxial side of the corolla lobes, *M. schaffneri* can be confused with *M. schlechtendalii* and *M. turneri*. *Metastelma schaffneri* is a species of western central Mexico, while *M. schlechtendalii* is distributed along the southern Gulf Coast, and *M. turneri* in northeastern Mexico. *Metastelma schlechtendalii* is best recognized by its pollinia, which are ovoid and attached to slightly geniculate caudicles, while the other two species have pyriform-reniform pollinia and s-shaped caudicles. *Metastelma schaffneri* has commonly much more slender leaves (to 12 mm wide) than *M. turneri* (to 18 mm wide) and a more slender gynostegium on a longer stipe (0.3–0.4 mm in contrast to 0.1–0.2 mm).

Wiggins 15628, the only specimen from Baja California, agrees quite well with *Metastelma schaffneri* with respect to leaf indumentum, subsessile inflorescences, corona exceeding the shortly stipitate gynostegium, and geniculate caudicles. However, corolla indumentum is very short (less than 100 μm), and the corona lobes attach along the stipe a little distant from the anthers.

Additional specimens examined. MEXICO. **Baja California:** Punta San Lorenzo, 25 mi. E of La Paz, 26 Nov. 1959 (fl), *Wiggins 15628* (ARIZ). **Durango:** Durango & vicinity, Apr.–Nov. 1896 (fl), *Palmer 159* (NY). **Guerrero:** en la piedra 22 km al E de Guayameo, 21 Mar. 1983 (fl), *Martínez 3634* (LL, WIS). **Jalisco:** near Guadalajara, 11 Nov. 1889 (fl), *Pringle 2749* (HBG). **Morelos:** Cuernavaca, 16 Nov. 1895 (fl), *Pringle 6205* (HBG, M, NY, P, S). **Nayarit:** Ahuacatlán, on slope S of town, 26 Jan. 1992 (fl), *Liede & Conrad 2962* (UBT). **Oaxaca:** 9 km al NE de Cuicatlán, rumbo a Concepción Pápalo, 23 Aug. 1980 (fl), *Mendraño 1630* (WIS); Santa Inez Mountains, 15 Oct. 1894 (fl), *Pringle 5626* (ARIZ, LL, NY); above Oaxaca, 7 Aug. 1895 (fl, fr), *Pringle 4766* (HBG, M, NY). **Puebla:** Rancho San Antonio, 10 km al NW de Molcaxac, 15 Oct. 1984 (fl), *Tenorio et al. 7660* (LL); vicinity of San Luis Tultitlanapa, near Oaxaca, June 1908 (fl), *Purpus 2617* (NY); Tehuacan, lava bed behind El Riego, 4 Aug. 1989 (fl), *Liede & Conrad 2604* (MO). **San Luis Potosí:** 1879, *Schaffner 313* (P). **Sinaloa:** NW base of Cerro Colorado, 4 Feb. 1940 (fl), *Gentry 5479* (MO, NY); Mesa Malqueson, Cerro Colorado, 8 Dec. 1939 (fl), *Gentry 5184* (ARIZ); Capadero, Sierra Tacuichamona, 12 Feb. 1940 (fl), *Gentry 5562* (ARIZ, NY); near roadside at Las Animas beach near Topolobambo, 28 Jan. 1964 (fl), *Turner s.n.* (LL). **Sonora:** Cañon de Bavispe, Aug. 1940 (fl), *White 3239* (NY). State unknown: 1905, *Purpus 1259* (NY).

14. Metastelma schlechtendalii Decne., in A. P. de Candolle, Prodr. 8: 513. 1844, non *Metastelma schlechtendalii* Chapm., Fl. South. U.S. 366. 1860, nom. illeg. *Cynanchum schlechtendalii* (Decne.) Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 226. 1947. TYPE: Mexico. Veracruz: Hacienda de la Laguna, Aug. 1828, *C. J. W. Schiede 159* (lectotype, designated by Stevens (2000: 256), P!; isotypes, HAL not seen, MO not seen, NY!, W not seen).

14a. Metastelma schlechtendalii Decne. var. **schlechtendalii.** Figures 22e, 23.

Metastelma decipiens Pittier, Contr. U.S. Natl. Herb. 13: 97. 1910, nom. illeg., non *Metastelma decipiens* Schltr., in Urban, Symb. Antill. 1: 249. 1899. TYPE: Guatemala. Quiché: San Miguel Uspatán, 2000 m, Apr. 1892, *E. T. Heyde & E. Lux 3060* (holotype, US not seen; isotypes, F not seen, M!, NY!, UPS!).

Metastelma parviflorum Schltdl., Linnaea 6: 731. 1831, nom. illeg., non *Metastelma parviflorum* R. Br. ex Schult., in Roemer & Schultes, Syst. Veg. 6: 120. 1820. TYPE: Mexico. Veracruz: Hacienda de la Laguna, Sep. 1828, *Schiede 260* (holotype, HAL!; isotype, HAL!).

Plants ascending, 80–150 cm high; *shoots* an-

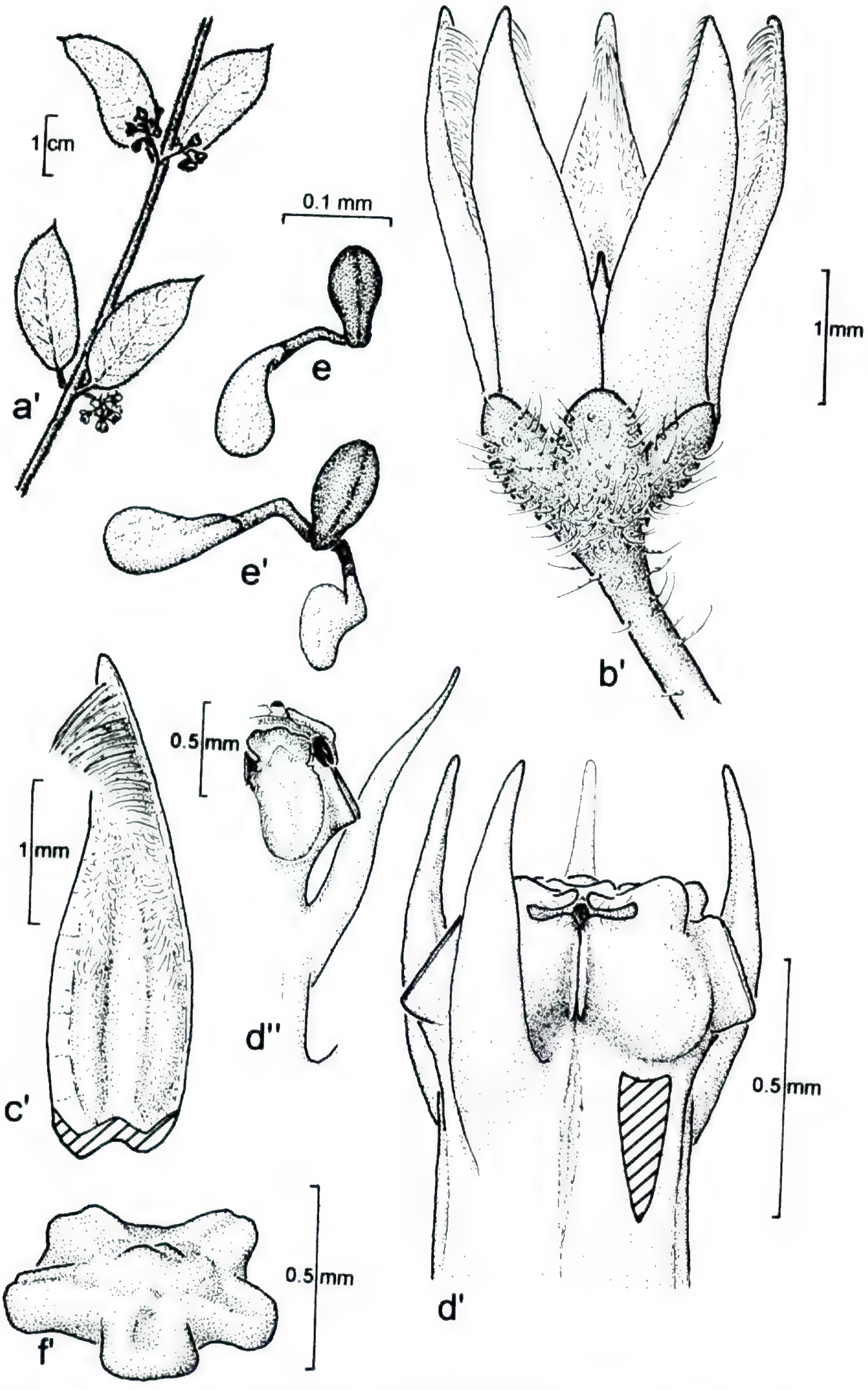


Figure 22. *Metastelma schlechtendalii*. a'–f': *M. schlechtendalii* var. *trichophyllum*. d'': *M. schlechtendalii* var. *arenicola*. e: *M. schlechtendalii* var. *schlechtendalii*. —a'. Shoot with inflorescences. —b'. Flower. —c'. Corolla lobe, adaxial view. —d, d''. Gynostegium and corona. —e, e'. Pollinarium. —f'. Style-head. a'–f': *Molina 13344*. d'': *Gentry 5431*. e: *Molina 15672*. Drawn by J. Conrad.

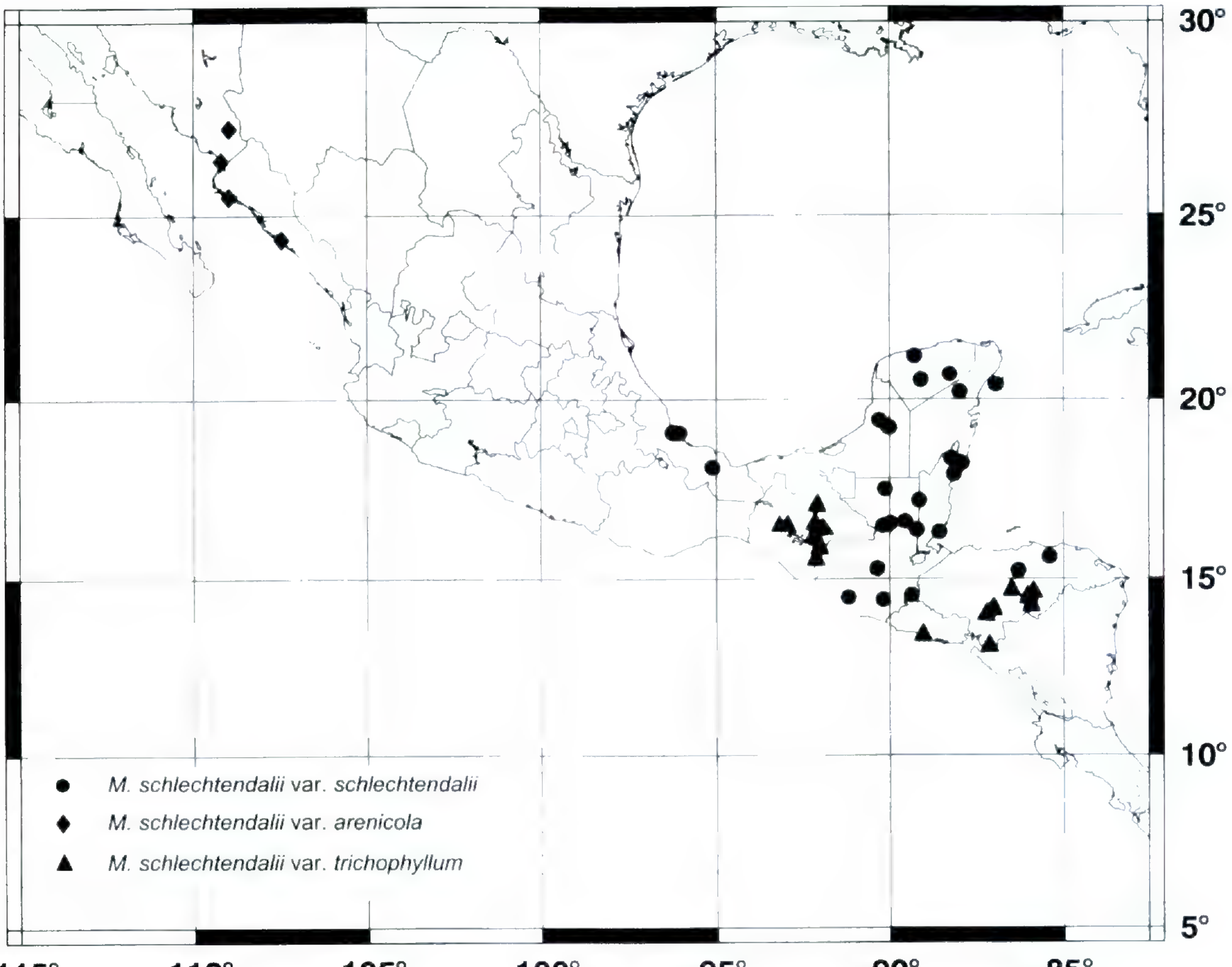


Figure 23. Distribution of *Metastelma schlechtendalii*.

nual, glabrous, sparsely to densely covered along a single line with recurved to flexuous trichomes, 150–300 μm long; internodes 2–5 cm long, 0.5–1 mm diam. *Leaves* with petioles 1–5(–10) mm long, with 0 to 2 colleters at blade base; blades 15–45 × 4–15 mm, elliptic to ovate, basally cuneate to rounded, apically acute to acuminate, adaxially glabrous or isolatedly to sparsely covered only on veins and margins (except for *Aguilar 124* with isolated trichomes on the lamina), with appressed trichomes, ca. 200 μm long, abaxially glabrous or very isolatedly covered mainly on veins and margins with appressed trichomes, 200–300 μm long. *Inflorescences* 2- to 12-flowered, all flowers open synchronously, sciadioidal, bostrychoid; *peduncles* (2–)4–15 mm long, glabrous, isolatedly to sparsely covered along a single line with recurved trichomes, 200–300 μm long. Flowers very sweetly fragrant; *floral bracts* 0.5–0.7 × 0.2–0.3 mm at the base, ovate, glabrous or ciliate; *pedicels* 1.5–2.5 mm long, glabrous, isolatedly to sparsely covered along a single line with recurved trichomes, 100–150 μm long. *Floral buds* ca. 2.5 mm long, ca. 1 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially with a few sparse trichomes mainly on the tube; calyx lobes ca. 1 × ca. 0.4 mm, ovate, apically acute; *corolla* campanulate, 2–3 mm long, abaxially white, glabrous, adaxially white, with verrucose trichomes, 150–200 μm long, on the apical and on the lateral parts of the lobes; lobes basally fused, 0.6–0.7 mm wide, erect to patent, ovate to lanceolate, apically acute; *gynostegial corona* 0.8–1 mm long, slightly longer than the gynostegium; lobes erect, attached along the stipe, laminar, triangular. *Gynostegium* ca. 0.5 mm high, ca. 1 mm diam., on a stipe 0.6–0.8 mm long; *anthers* broader than high, rectangular, abaxially planar; anther wings 150–200 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther; connective appendages ca. 200 μm long, ca. 150 μm wide, ovate, narrower than the stamen, strongly inflexed; *pollinarium* with corpusculum 120–150 μm long, between 1.5 times and twice as long as broad, ovoid; caudicles 100–130 μm long, cylindrical, slightly geniculate; pollinia apically at-

tached to the caudicles, 150–180 μm long, 80–100 μm wide, ovate in cross section, clavate; *style-head* white, 0.5–0.6 mm diam., ca. 0.25 mm high, upper part 0–0.1 mm high, shorter than the lower part, flat to umbonate. *Follicles* one per flower, 35–40 mm long, 2–3 mm diam., fusiform, terete, apically strongly beaked, dark brown, glabrous; *seeds* ca. 5.5 mm long, ca. 3 mm wide, oblong, light brown, seta side tuberculate, aseta side smooth, marginally with 0.5 mm wide wing with irregularly denticulate margin; coma ca. 20 mm long.

Phenology. Collected in flower from July to April; in fruit in November.

Distribution. Belize: Corazal, Orange Walk, Toledo; Guatemala: Guatemala, Jutiapa, Quetzaltenango, Quiché; Honduras: Colón, Ocotepeque; Mexico: Campeche, Quintana Roo, Veracruz, Yucatán; very wide ecological amplitude, sand dunes, salt marshes, roadside vegetation, thickets, disturbed forests; sea level to 2000 m.

Literature and illustrations. Pitter (1910: fig. 4a, b).

Williams (1968) included *Metastelma decipiens* Pittier in the synonymy of *M. schlechtendalii* var. *schlechtendalii* because they share narrowly oblong-lanceolate corolla lobes that are adaxially densely barbellate, a corona attached along the stipe and slightly exceeding the gynostegium, and lanceolate or ovate-lanceolate leaves with trichomes only on veins and margins.

Metastelma schlechtendalii var. *schlechtendalii* is a frequent species especially in lowland areas around the Yucatán Peninsula and up to 2000 m in Guatemala and Honduras. In the Yucatán, it is often difficult to distinguish from short-stiped, only vaguely barbate specimens of *M. barbigerum* var. *liesnerianum*, but the transversely oblong outline of the gynostegium is diagnostic against the conical gynostegium of the *M. barbigerum* complex. However, there seems to be a lot of hybridization and introgression between the two species complexes especially in the Yucatán, judging from the numerous specimens with somewhat intermediate characters.

Metastelma schlechtendalii var. *schlechtendalii* is easily confused with *M. schaffneri* and *M. turneri*, but can be distinguished by its conspicuously protruding anther wings (short and almost vertical in the other two species), and its flat-topped gynostegium with strongly inflexed anther appendages (rounded to slightly conical gynostegium with slightly inflexed anther appendages in the other two species).

Metastelma schlechtendalii var. *schlechtendalii* has often been confused with *M. parviflorum* R. Br. ex Schult., a widespread taxon in northern South America and the Caribbean, but it is clearly distinguishable by its only basally fused corolla and the corona lobes attached along the stipe, and not, as in *M. parviflorum*, at the base of the stipe, fused to the corolla. However, Schlechtendal (1831: 731) commited exactly this error in his brief enumeration. Two years later (Schlechtendal, 1833: 518), he indicated the specimen on which he based his conclusion, *Schiede 260*, collected at the same locality as the lectotype of *M. schlechtendalii*, *Schiede 159*. Decaisne (1844) noted the error, and TROPICOS takes the same view.

Additional specimens examined. BELIZE. **Corazal:** ca. 4 km SE of Sarteneja, 18 Mar. 1987 (fl), *Davidse & Brant 32667* (LL, NY). **Orange Walk:** Honey Camp, 29 Oct. 1929 (fl), *Lundell 651* (NY). **Toledo:** Monkey River, Swansea branch, 26 Nov. 1941 (fl), *Gentle 3815* (LL, NY). GUATEMALA. **Guatemala:** along Hwy. 18 about 7.2 mi. E of San José Piñula, 16 July 1971 (fl), *Stevens 1250* (NY, TEX). **Jutiapa:** Mongoy, Laguna de Guija, Apr. 1894 (fl), *Heyde & Lux 6348* (M, NY). **Petén:** La Libertad, 2 June 1933, *Lundell 3562* (WIS); Poptun Road, km 82, 21 Nov. 1967 (fl), *Contreras 7237* (LL); Santa Ana, 20 km al E de Santa Elena, 13 Nov. 1965 (fl), *Molina 15672* (NY); alrededor de Libertad, 30 km de Santa Elena, 22 Jan. 1970 (fl), *Tún Ortíz 604* (NY); Santa Elena, en el camino para Santa Marta, a km 3, lado N, 12 Dec. 1970 (fl), *Tún Ortíz 1494* (NY); San Miguel, Savanna San Miguel, 3 km N of San Miguel, 8 Dec. 1967 (fl), *Contreras 7270* (LL); Tikal Nat. Park, Bajo de Santa Fé, salida de Arroyo Corriental, 17 Jan. 1964 (fl), *Contreras 3866* (LL). **Quetzaltenango:** Palmar, 13 Oct. 1934 (fl), *Skutch 1438* (NY). District not known: St. Tomas, 1841, *Friedrichsthal s.n.* (NY). HONDURAS. **Colón:** 1.8 mi. strip on N bank of Río Guaimoreto, NE of Trujillo on old rd. to Castilla, 11 Dec. 1980 (fl), *Saunders 740* (LL, NY). **Ocotepeque:** El Cerro, vicinity of San Antonio, 30 Aug. 1968 (fl), *Molina 22442* (NY); along Lempa river, rd. to Esquipulas, 29 Aug. 1968 (fl), *Molina 22438* (NY). MEXICO. **Campeche:** alrededores de las grutas de Xtacumbilxunam, a 3 km al O de Bolonchen de Rejón, 29 Sep. 1985 (fl), *Cabrera & De Cabrera 9505* (NY); Zona militar, cd de Campeche, 28 Oct. 1997 (fl), *Gutiérrez 5462* (TEX). **Quintana Roo:** en la desviación a Laguna Ocum, a 10 km al Sur de GF. Carrillo Puerto, 13 Nov. 1980 (fl), *Cabrera & Cortez 281* (NY); Punta Bete, donde está el Hotel Capitán Lafitte, 6 Jan. 1980 (fl), *Sousa et al. 10929* (NY). **Veracruz:** Mpo. Alto Lucero, Boca Andrea, 15 Oct. 1971 (fl), *Dorantes 385* (TEX); Hacienda de la Laguna, *Schiede 11* (HAL); Veracruz, *Wawra 625* (NY); Zacuapan and vicinity, Nov. 1906 (fl), *Purpus 2094* (NY). **Yucatán:** 30 mi. E of Mérida at Hoctun, 7 Mar. 1973 (fl), *Butterwick 78* (TEX); Uayma, ca. 20 km NW von Valladolid, 21 Nov. 1981 (fl, fr), *Flügel & Geiseler 7016* (B), Feb. 1916 (fl), *Gaumer 23436* (NY); Progreso, E of port, July 1938 (fl), *Lundell & Lundell 8113* (TEX); along dirt rd. to Chamul SW of village, 14 Oct. 1989 (fl), *Mogensen 1151* (NY). State unknown: *Berlandier s.n.* (NY).

14b. Metastelma schlechtendalii Decne. var. **arenicola** Liede & Meve, var. nov. TYPE: Mexico. Sonora: Mesa Masiaca, just N of the microwave tower, 6.5 km (by air) WNW of San José de Masiaca, ca. 200 m, 22 Nov. 1993, *V. W. Steinmann 93-358* (with *C. D. Bertelsen, S. A. Meyer, K. J. Johnson, M. M. Steinmann, T. R. van Devender & J. F. Wiens*) (holotype, ARIZ!). Figures 22d″, 23.

Haec varietas varietati *schlechtendalii* similis, sed differt inflorescentibus subsessilibus, bracteis sepalibusque lanceolatis, corona staminali gynostegium multo superante.

Plants ascending; *shoots* perennial, basally woody, with grayish brown bark, sparsely covered along a single line or over the entire surface (*Gentry 5431*) with erect or recurved trichomes, 200–250 μm long; internodes 2–4 cm long, 0.5–1 mm diam. *Leaves* with petioles 2–5 mm long, with 0 to 2 colleters at blade base; blades 5–25(–50) × 4–10 mm, ovate to linear, basally rounded to cuneate, apically acute to acuminate, adaxially isolatedly to sparsely covered only on the midrib and margins with recurved trichomes, 150–200 μm long, abaxially glabrous. *Inflorescences* always one per node, extraaxillary, 3- to 8-flowered, 2 to 7 flowers open synchronously, sciadioidal, subsessile, rarely pedunculate with peduncles to 4 mm long, densely covered along a single line with recurved trichomes, 150–200 μm long; *floral bracts* 0.7–1 × 0.2–0.3 mm at the base, lanceolate, glabrous; *pedicels* 1.5–3 mm long, sparsely to densely covered along a single line with recurved trichomes, 100–150 μm long, rarely glabrous. *Floral buds* ca. 2.5 mm long, ca. 1.2 mm diam.; *calyx* basally fused, campanulate, abaxially with a few sparse trichomes, mainly on the tube; calyx lobes 0.8–1.3 × 0.3–0.5 mm, lanceolate, apically acute; *corolla* campanulate, 2.5–3 mm long, abaxially white, glabrous, adaxially white, with smooth trichomes, 100–150 μm long, on the apical and on the lateral parts of the lobes; lobes basally fused, 0.5–0.7 mm wide, erect to patent, ovate, apically acute; *gynostegial corona* 1.2–1.5 mm long, distinctly longer than the gynostegium; lobes erect to inflexed, attached along the stipe, laminar, triangular. *Gynostegium* 0.7–0.8 mm high, 0.3–0.4 mm diam., on a stipe 0.5–0.6 mm long; *anthers* broader than high, rectangular, abaxially planar; anther wings 200–250 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other; connective appendages ca. 500 μm long, ca. 300 μm wide, ovate, narrower than the stamen, slightly to strongly inflexed; *pollinarium* with corpusculum ca. 150 μm long, between 1.5 times and twice as long as broad, ovoid; caudicles ca. 80 μm long, cylindrical, slightly geniculate; pollinia apically attached to the caudicles, ca. 180 μm long, ca. 80 μm wide, ovate in cross section, ovoid; *style-head* white, ca. 0.7 mm diam., 0.4–0.5 mm high, upper part ca. 0.2 mm high, equaling the lower part, distinctly umbonate or flat (*Gentry 5431*). *Follicles* one per flower, 35–45 mm long, 4–5 mm diam., obclavate, terete, apically shortly beaked, dark brown to black, glabrous; *seeds* 5–6 mm long, 3–4 mm wide, ovate, medium brown, seta and aseta side tuberculate, papillose with regularly arranged papillae, marginally wingless, denticulate; coma 20–30 mm long, yellowish.

Phenology. Collected in flower in January, and from September to November; in fruit in October.

Distribution. Mexico: Sinaloa, Sonora; littoral sand hills, basaltic slopes, thornscrub and thorn forest; 30–400 m.

In addition to the diagnostic characters of the new variety (subsessile inflorescences, lanceolate bracts and calyx lobes, and a corona considerably exceeding the gynostegium), the majority of specimens (70%) have a slightly elevated style-head, while the style-head is flat to slightly umbonate in the other two varieties throughout. The variety is restricted to the western Mexican lowlands, separated by at least 1000 km from the other two varieties.

Gentry 5431 does not fit the description of *Metastelma schlechtendalii* var. *arenicola* perfectly; its shoots are sparsely, but evenly, covered with trichomes (in all other specimens, the trichomes only occur along a single, though occasionally rather broad, line), floral bracts and sepals are comparatively short, the flowers relatively large, and the style-head is flat. Nevertheless, gynostegium shape and the protruding anther wings make it a member of the *M. schlechtendalii* complex and it is best accommodated here.

Paratypes. MEXICO. **Sinaloa:** Altata, 31 Jan. 1940 (fl), *Gentry 5431* (ARIZ, NY); Topolabampo, 10 Oct. 1962 (fl), *Skorepa 173* (WIS); nr. Yacht Hotel, Topolobampo, 5 Oct. 1964 (fr), *Turner & Hastings 64-128* (ARIZ). **Sonora:** summit of Cerro Prieto, vic. of microwave station, 15 km E of Navojoa above rd. to Alamos, 5 Sep. 1989 (fl), *Sanders 9265* (ARIZ); Mesa Masiaca vicinity, at summit of M.M. microwave tower, 6.5 km (by air) ENE of San Jose de Masiaca, 23 Sep. 1994 (fl), *Friedman 379-94* (ARIZ).

14c. Metastelma schlechtendalii Decne. var. **trichophyllum** (L. O. Williams) Liede & Meve, comb. et stat. nov. Basionym: *Cynanchum trichophyllum* L. O. Williams, Fieldiana, Bot. 32: 41. 1968. *Metastelma trichophyllum*

(L. O. Williams) W. D. Stevens, Phytologia 64: 335. 1988. TYPE: Honduras. Olancho: Cerca de Río Telica, camino de Montaña Uval, 20 Nov. 1963, *A. Molina R. 13344* (holotype, F!; isotypes, EAP not seen, NY! TEX!). Figures 22a′–f′, 23.

Plants ascending, to 500 cm high; *shoots* perennial, basally woody, with grayish brown bark, densely covered over the entire surface or along a single line with erect trichomes, 300–400 μm long; internodes 2–5 cm long, 1 mm diam. *Leaves* with petioles 2–5 mm long, with 2 colleters at blade base; blades 15–35 × 7–15 mm, ovate, basally rounded, apically acute to acuminate, adaxially and abaxially sparsely covered over the entire surface with erect trichomes, 250–300 μm long. *Inflorescences* always one per node, (4–)6- to 12-flowered, 4 to 8 flowers open synchronously, sciadioidal; *peduncles* 5–15 mm long, densely covered over the entire surface or along a single line with erect to recurved trichomes, 300–400 μm long; *floral bracts* 0.35–0.4 × 0.2–0.3 mm at the base, ovate, ciliate; *pedicels* 3–5 mm long, sparsely to densely covered over the entire surface with erect trichomes, 300–400 μm long. *Floral buds* 2–2.3 mm long, 1–1.2 mm diam., ovoid; *calyx* basally fused, campanulate; calyx lobes ca. 0.8 × ca. 0.3 mm, ovate, apically acute; *corolla* cyathiform to campanulate, 2.5–3(–4) mm long, abaxially cream to yellow, glabrous, adaxially white, with verrucose trichomes, to 200 μm long, on the apical and on the lateral parts of the lobes; lobes basally fused, 0.5–0.7 mm wide, patent, ovate, apically acute; *gynostegial corona* 0.8–1 mm long, equaling to longer than the gynostegium; lobes erect, attached along the upper third of the stipe, lanceolate, extended into a filiform tip. *Gynostegium* ca. 0.4 mm high, 0.8–1 mm diam., on a stipe 0.6–1 mm long; *anthers* broader than high, rectangular, abaxially planar; anther wings 200–300 μm long, extending along the entire length of the anther, anther wings of adjacent anthers parallel to each other, in the same plane as the anther; connective appendages ca. 250 μm long, ca. 150 μm wide, ovate, narrower than the stamen, strongly inflexed; *pollinarium* with corpusculum 120–150 μm long, between 1.5 times and twice as long as broad, ovoid; caudicles 100–120 μm long, cylindrical, slightly geniculate; pollinia apically attached to the caudicles, 180–200 μm long, 80–100 μm wide, ovate in cross section, clavate; *style-head* white, 0.5–0.6 mm diam., ca. 0.25 mm high, upper part flat. *Follicles* (*fide* protologue) 25–50 mm long, 4–5 mm diam., obclavate, terete, apically strongly beaked, wingless, with dense indumentum; *seeds* not seen.

Phenology. Collected in flower from August to November.

Distribution. El Salvador; Honduras: Morazán, Olancho; Mexico: Chiapas; matorral, secondary vegetation, tropical deciduous forest; (500–)800–2100 m.

Metastelma schlechtendalii var. *trichophyllum* is easily separated from the typical variety by the dense, equally distributed indumentum on stems and leaves. In addition, inflorescences appear to bear more flowers in variety *trichophyllum*, a character hard to judge from herbarium specimens, as they might not have been picked at the peak of flowering. The distribution area of variety *trichophyllum* is disjunct between Chiapas (Mexico) and Honduras–El Salvador, with a gap in Guatemala, where the typical variety colonizes even the higher elevations. In Honduras, the typical variety and variety *trichophyllum* both occur, but variety *trichophyllum* seems to prefer higher altitudes there. However, as the floral characters fully agree with those of the *M. schlechtendalii* complex and the distribution areas of the typical variety and variety *trichophyllum* are continuous to somewhat overlapping in Honduras, varietal (rather than specific or subspecific) rank for the taxon is appropriate, even though it is one of the easiest *Metastelma* taxa to recognize in the field by virtue of the equally distributed indumentum on the leaves.

Additional specimens examined. EL SALVADOR. San Salvador, 1922, *Calderón 1271* (NY). HONDURAS. **Morazán:** along quebrada El Chorrito, Cerro de Hule 20 km S of Tegucigalpa, 27 Oct. 1966 (fl), *Molina 18455* (NY); Ojojona, 45 km S de Tegucigalpa, 28 Sep. 1985 (fl), *Aspra 65* (B); near Río Guacerique & Los Laureles, NW of Tegucigalpa, 4 Nov. 1966 (fl), *Molina 18607* (NY). **Olancho:** Carretera y margen del Río Juticalpa, 6 km de Juticalpa, 18 Nov. 1963, *Molina 13226* (NY, TEX); Valle Lepaguare entre El Zarzal y empalme a Galeras, 21 Nov. 1963 (fl), *Molina 13370* (NY). MEXICO. **Chiapas:** rd. from El Bosque to Simojovel, 10 Oct. 1967 (fl), *Ton 3092* (TEX); near microwave station of La Mina, 12 km S of MEX 190 nr Rizo de Oro, 16 Oct. 1971 (fl), *Breedlove & Thorne 20658* (TEX); a 22 km al N de Ocozocuautla camino a Malpaso, 24 Oct. 1985 (fl), *Martínez 14284* (LL); 10 km SW of Ocosingo along rd. to San Cristóbal, 23 Sep. 1972 (fl), *Breedlove 27820* (NY, TEX); Puebla Nueva, 21 Oct. 1987 (fl), *Pérez 85* (NY, TEX); Colonia Choro, 15 Nov. 1966 (fl), *Ton 1548* (TEX); La Roblada, Ocozocoautla, 15 Nov. 1971 (fl), *MacDougal H116* (NY); Las Rosas on rd. to Venustiano Carranza, 8 Aug. 1965 (fl), *Roe et al. 997* (paratype, NY, WIS); 15 km SW of Suchiapa along rd. to Villa Flores, 3 Oct. 1972 (fl), *Breedlove 28258* (NY, TEX).

15. Metastelma stenomeres (Standl. & Steyerm.) W. D. Stevens, Phytologia 64: 335. 1988.

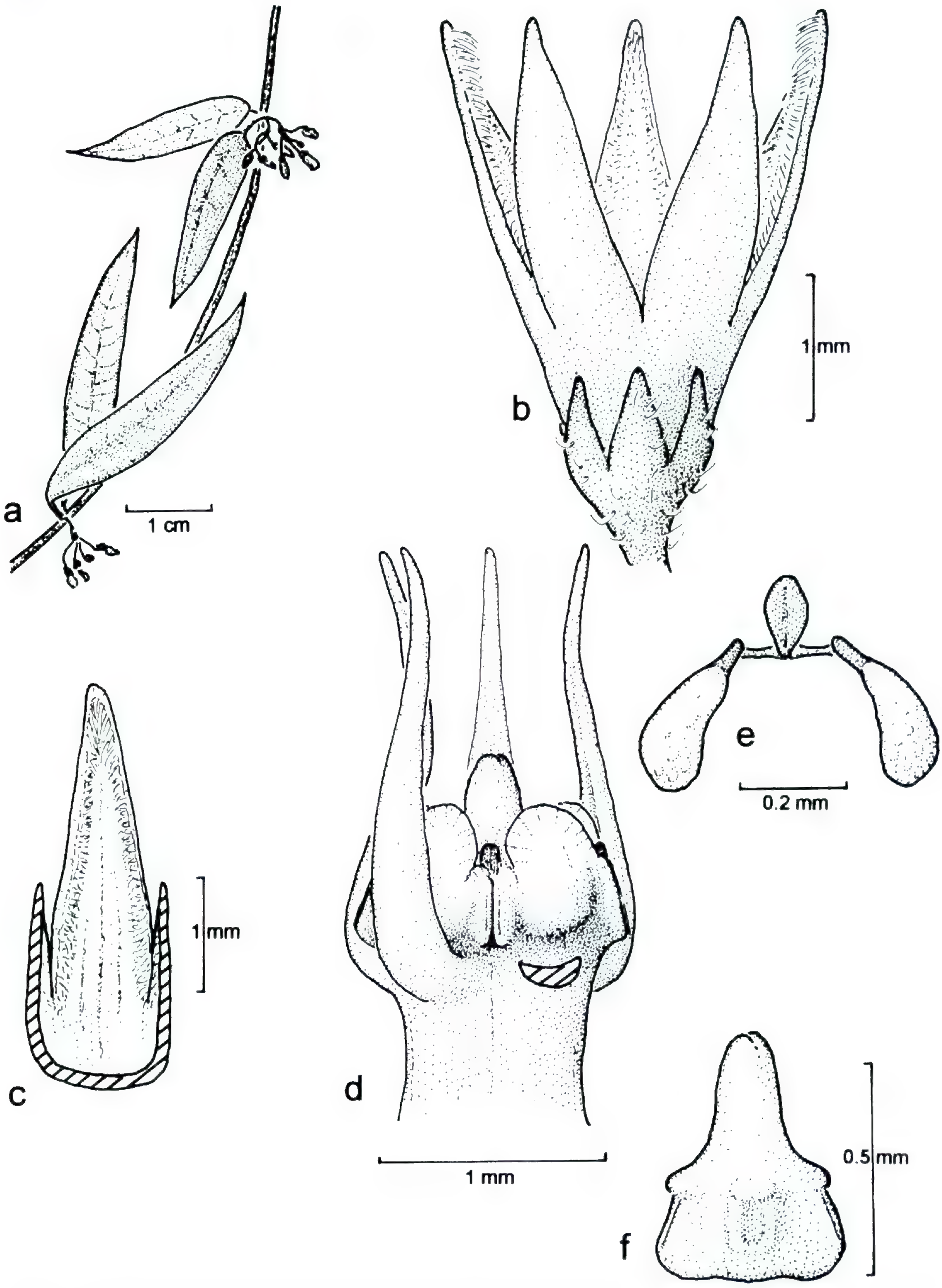


Figure 24. *Metastelma stenomeres.* —a. Shoot with inflorescences. —b. Flower. —c. Corolla lobe, adaxial view. d. Gynostegium and corona. —e. Pollinarium. —f. Style-head. a–f: *Schipp 674.* Drawn by J. Conrad.

Cynanchum stenomeres Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 224. 1947. TYPE: Belize. All Pines, 2 m, 5 Feb. 1930, *W. A. Schipp 674* (holotype, F not seen; isotype, NY!). Figures 12, 24a–f.

Plants ascending, 50–150 cm high; *shoots* perennial, glabrous; internodes 4–6 cm long, ca. 1 mm diam. *Leaves* with petioles 4–6 mm long, with 0 or 1 colleter at blade base; blades 25–50 × 5–9 mm, slenderly elliptic or lanceolate, basally acute to cuneate, apically acute to acuminate, adaxially and abaxially glabrous. *Inflorescences* occasionally two per node, extra-axillary, 8- to 12-flowered, all flowers open synchronously, sciadioidal, but sometimes basally dichasial; *peduncles* 3–5 mm long, sparsely to densely covered along a single line with recurved trichomes, 100–200 μm long. *Flowers* sweetly fragrant; *floral bracts* 0.4–0.6 × 0.2–0.3 mm at the base, ovate, glabrous; *pedicels* 3–5 mm long, glabrous. *Floral buds* 3.5–4 mm long, 1.2–1.5 mm diam., slender ovoid; *calyx* basally fused to fused for ca. ⅓ of its length, campanulate, abaxially very sparsely covered with trichomes; calyx lobes 0.6–0.8 × 0.2–0.4 mm, ovate, apically acute to obtuse; *corolla* salverform, 4–4.5 mm long, abaxially white, glabrous, adaxially white, adaxially with verrucose trichomes, to 300 μm long, on the lateral parts of the lobes; lobes fused for ca. ⅓ of total corolla length, 0.8–1 mm wide, erect to patent, slenderly ovate, apically obtuse; *gynostegial corona* 2 mm long, longer than the gynostegium; lobes erect, attached directly underneath the anthers, laminar to filiform, lanceolate, extended into a long, slender tip. *Gynostegium* ca. 1.3 mm high, 0.7 mm without appendage of style-head, ca. 0.8 mm diam., on a column ca. 1.3 mm long; *anthers* broader than high, rectangular, abaxially planar; anther wings 0.3 μm long, extending along the entire length of the anther, in the same plane as the anther; connective appendages 150 μm long, 300 μm wide, ovate, narrower than the stamen, strongly inflexed; *pollinarium* with corpusculum ca. 150 μm long, between 1.5 times and twice as long as broad, ovoid; caudicles ca. 150 μm long, cylindrical, geniculate; pollinia apically attached to the caudicles, ca. 200 μm long, ca. 100 μm wide, elliptical in cross section, pyriform; *style-head* white, ca. 0.4 mm diam., ca. 0.6 mm high, upper part ca. 0.4 mm high, equaling or longer than the lower part, obinfundibuliform or conical. *Follicles* one per flower, ca. 50 mm long, 4 mm diam., obclavate, terete, apically strongly beaked, light gray-brown, wingless, glabrous; *seeds* unknown.

Phenology. Collected in flower in February and from August to October.

Distribution. Belize; in open pine forests, hammock edges; lowlands.

A well-distinguished species endemic to Belize, which is most easily recognized by its floriferous inflorescences, the slender outline of the flowers, the very long (to 2 mm), acute and membraneous corona lobes, the long (to 1.3 mm) and slender column carrying corona and gynostegium, and the usually pronounced central elongation (to 0.4 mm) of the style-head.

Additional specimens examined. BELIZE. Broken Ridge, 8 mi. NE of Boomtown, 17 Sep. 1936, *O'Neill 8660* (NY, WIS); near Manatee, 15 Oct. 1940 (fl), *Gentle 3417* (NY, TEX); Monkey River, nr. Jenkins Creek, 28 Sep. 1942 (fl), *Gentle 4190* (NY, TEX); Mountain Pine Ridge, San Agustin, July–Aug., 1936 (fl), *Lundell 6656* (NY, TEX, WIS); Mullins River rd., 15 Nov. 1954 (fr), *Gentle 8458* (TEX); Tracie Rock, Sibun River, 10 Aug. 1935 (fl), *Gentle 1755* (NY, WIS).

16. Metastelma turneri Liede & Meve, nom. et stat. nov. Basionym: *Cynanchum maccartii* Shinners var. *latifolium* Turner ex Henrickson, Sida 12: 98. 1987, non *Metastelma latifolium* Rose, Contr. U.S. Natl. Herb. 1: 106. 1891. TYPE: Mexico. Nuevo León: Las Anacuas, Mpio. Linares, 640 m, 5 Aug. 1980, *G. S. Hinton 17935* (holotype, TEX not seen). Figures 15, 25a–f.

Plants ascending, 150–200 cm high; *shoots* perennial, basally slightly woody, with greenish to yellowish brown bark, sparsely covered along a single line with recurved trichomes, 200–350 μm long; internodes 2–5 cm long, ca. 1 mm diam. *Leaves* with petioles 2–10 mm long, with 1 or 2 colleters at blade base; blades 10–40(–50) × 5–18 mm, ovate to lanceolate, basally rounded, apically acuminate, marginally revolute (when dry), adaxially isolatedly to sparsely covered, mainly or only on the midrib and margins with recurved trichomes, 150–250 μm long, abaxially glabrous or with a few recurved trichomes on the midvein. *Inflorescences* always one per node, extra-axillary, 3- to 8-flowered, 2 or 3 flowers open synchronously, sciadioidal, subsessile; *floral bracts* 0.4–0.7 × 0.2–0.3 mm at the base, lanceolate, ciliate; *pedicels* 2–4 mm long, covered along a single line with recurved trichomes, 200–250 μm long. *Floral buds* ca. 3 mm long, ca. 1.5 mm diam., ovoid; *calyx* basally fused, campanulate, abaxially glabrous or slightly verrucose, ciliate; calyx lobes 0.5–1 × 0.3–0.5 mm, ovate, apically rounded; *corolla* subcampanulate, 2.5–4.0 mm long, abaxially creamish white, gla-

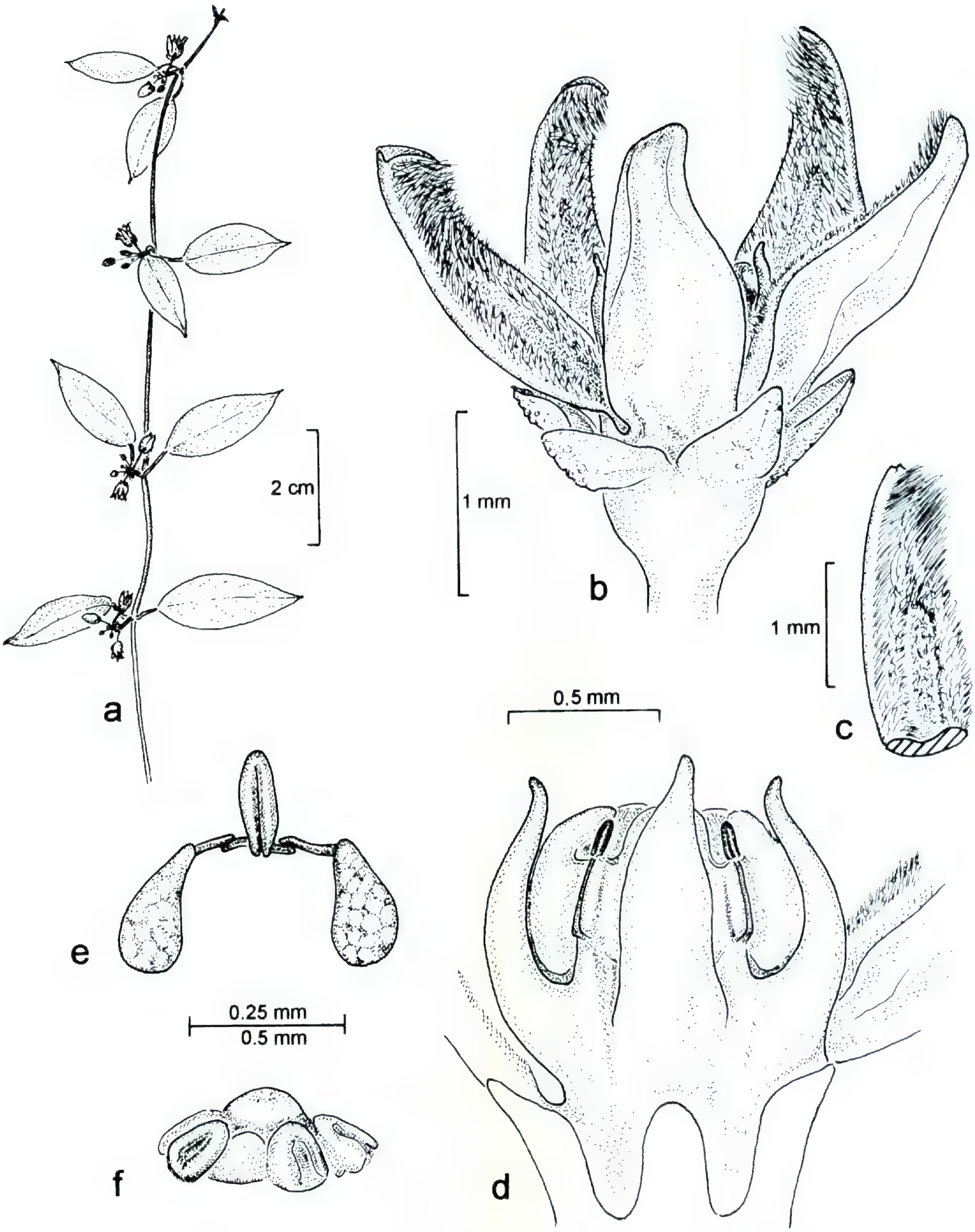


Figure 25. *Metastelma turneri*. —a. Shoot with inflorescences. —b. Flower. —c. Corolla lobe, adaxial view. —d. Gynostegium with corona. —e. Pollinarium. —f. Style-head. a: *Hinton 17776*. b–f: *Pringle 11841*. Drawn by U. Meve.

brous, adaxially creamish white, with smooth trichomes, 50–200 μm long, on the apical and on the lateral parts of the lobes, apical trichomes longer than lateral ones, and scattered deflexed hispid trichomes on the central parts of the lobes; lobes basally fused, 0.7–1 mm wide, patent, ovate to lanceolate, apically acute; *gynostegial corona* 0.7–1 mm high, equaling to longer than the gynostegium; lobes erect, apically slightly reflexed, attached directly underneath the anthers, laminar, ovate. *Gynostegium* 0.6–1 mm high, 0.5–0.8 mm diam., on a stipe 0.1–0.2 mm long; *anthers* longer than broad,

trapezoidal, abaxially rounded; anther wings 200–250 μm long, not extending along the entire length of the anther; anther wings of adjacent anthers parallel to each other, slightly centrifugal; connective appendages 200–250 μm long, 250–300 μm wide, ovate, narrower than the stamen, slightly inflexed; *pollinarium* with corpusculum 100–150 μm long, between 1.5 times and twice as long as broad, elliptic; caudicles ca. 100 μm long, cylindrical, strongly s-shaped, convex-concave; pollinia apically attached to the caudicles, 180–220 μm long, ca. 100 μm wide, ovate in cross section, pyriform; *style-head* white, 0.5–0.7 mm diam., 0.2–0.3 mm high, upper part ca. 0.1 mm high, shorter than the lower part, flat to umbonate. *Follicles* 45–55 mm long, 5–6 mm diam., terete, apically strongly beaked, dark brown, glabrous; *seeds* 6–7.5 mm long, 3–4 mm wide, ovate, dark brown, seta and aseta side smooth, marginally with 0.5–0.7 mm wide wing with slightly irregular margin; coma ca. 20 mm long.

Phenology. Collected in flower in May, July, August, and October; in fruit in October.

Distribution. Mexico: Nuevo León, San Luis Potosí, Tamaulipas; on dry hillslopes in scrub; 400–2000 m.

Literature and illustrations. Henrickson (1987: 98, fig. 1).

Henrickson (1987) considered *Metastelma turneri* a variety of *M. palmeri*, with which it shares the general shape of the corona. However, not only are the leaves and the flowers of *M. turneri* usually larger than those of *M. palmeri* (leaves: 16–35 × 2.5–7 mm vs. 10–40(–50) × 5–18 mm, flowers: up to 4 mm vs. up to 3 mm, respectively), but also the indument of the adaxial side of the corolla lobes in *M. turneri* is more reminiscent of *M. schlechtendalii* than of *M. palmeri* with the apical trichomes conspicuously longer than the lateral ones.

A new name has to be chosen for this species because *Metastelma latifolium* Rose (1891) has priority.

One specimen (Mexico. Tamaulipas: rd. to Bustamente N of La Presita & 2.7 mi. N of Hwy. 70, 21 May 1982 (fl), *Dorr 2359*, TEX) shows the corolla lobe indumentum of *Metastelma turneri*, but the leaf shape and flower size of *M. palmeri* and is assumed to be a hybrid between the two species.

Additional specimens examined. MEXICO. **Nuevo León:** El Chipinque, ca. 6 km al sur de Monterrey, camino a la meseta, 7 Oct. 1998 (fl, fr), *Villarreal & Carranza s.n.* (TEX); Linares, 12 May 1980 (fl), *Rzedowski 17776* (TEX); Sierra Madre above Monterrey, 17 Aug. 1903 (fl), *Pringle 11841* (TEX); Montemorelos, 10 Aug. 1988 (fl), *Patterson 6476* (TEX); Villa Santiago, Cañon de Potrero Redondo, 4 July 1935 (fl), *Mueller 2099* (NY, TEX). **San Luis Potosí:** 75 km N of San Luis Potosí, on side rd. to Gauadalcázar at km 11 ½, 19 July 1982 (fl), *Fryxell 3820* (NY). **Tamaulipas:** 12 km NW of Palmillas on rd. to Miquihuana, 14 Aug. 1941 (fl), *Stanford et al. 920* (NY *2341*); Mpio. Victoria, Altas Cumbres, 29 June 1985 (fl), *Hernandez 1534* (TEX).

Excluded Names

Metastelma angustifolium Turcz., Bull. Soc. Imp. Naturalistes Moscou 1852(2): 315. 1852. TYPE: Mexico. Miradores, alt. 3000 ped.", *J. Linden 1353* (holotype, P!).

A member of the genus *Orthosia*.

Metastelma eulaxiflorum (Lundell) Liede, Novon 7: 41. 1997. *Cynanchum eulaxiflorum* Lundell, Wrightia 5: 351. 1977. *Jobinia eulaxiflora* (Lundell) W. D. Stevens, Novon: 244. 2000. TYPE: Guatemala. Baja Verapaz: Union Barrios, high forest hilltop, E of km 154, 8 June 1975, *C. L. Lundell & E. Contreras 19401* (holotype, LL!; isotypes, MO not seen, S!).

Transferred to the previously exclusively South American genus *Jobinia* E. Fourn. by Stevens (2000) because of its paired, axillary, diffusely paniculate inflorescences.

Metastelma filisepalum Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 956. 1938. *Cynanchum filisepalum* (Standl.) L. O. Williams, Fieldiana, Bot. 32: 36. 1968. TYPE: Costa Rica. Entre San Ramón y La Palma de San Ramón, June 1928, *A. M. Brenes 6179* (holotype, F not seen; isotype, NY!).

This species is the only presently known member of the genus *Scyphostelma* Baill. (formerly "*Cynanchum*" sect. *Microphyllum*) in Central America because of its basally fused corona and its characteristic branching pattern of long shoots and short shoots bearing distichously arranged leaves.

Metastelma glaberrimum Woodson, Ann. Missouri Bot. Gard. 107: 17. 1937. *Cynanchum glaberrimum* (Woodson) L. O. Williams, Fieldiana, Bot. 32: 36. 1968. TYPE: Panama. Chiriquí: valley of the upper Río Chiriquí Viejo, near Monte Lirio, ca. 1830 m, 11 July 1935, *R. J. Seibert 300* (holotype, MO!, isotype, MO not seen).

A member of the genus *Orthosia* because of its basally fused corona and adaxially glabrous corolla lobes.

Metastelma miserum (L. O. Williams) W. D. Stevens, Phytologia 64: 335. 1988. *Cynanchum miserum* L. O. Williams, Fieldiana, Bot. 32: 38. 1968. TYPE: Guatemala. Alta Verapaz: Im Walde in Pansamala, alt. 1260 m, July 1887, *H. v. Tuerckheim 1290* (holotype, US!; isotypes, F not seen, GH not seen, P!).

A member of the genus *Orthosia* because of its basally fused corona and adaxially glabrous corolla lobes.

Metastelma pubescens (Greenm.) W. D. Stevens, Phytologia 53: 405. 1983. *Astephanus pubescens* Greenm., Proc. Amer. Acad. Arts 32: 299. 1897. SYNTYPES: Mexico. Morelos: wet barranca above Cuernavaca, 2100 m, 21 Sep. 1896, *C. G. Pringle 6507* (F!, GH!, P! MO not seen, NY!); "in the mountains near Cuernavaca," 3 Aug. 1896, *C. G. Pringle 7203* (GH!).

A member of the genus *Orthosia* because of its adaxially papillate (but not indumented) corolla lobes, green stems, double inflorescences, and twin follicles.

Metastelma rubens (L. O. Williams) W. D. Stevens, Phytologia 64: 335. 1988. *Cynanchum rubens* L. O. Williams, Fieldiana, Bot. 32: 39. 1968. TYPE: Guatemala. Chimaltenango: Santa Elena, 2400–2700 m, 27 July 1933, *A. F. Skutch 503* (holotype, US!; isotype, NY!).

A member of the genus *Orthosia* because of its basally fused corona and adaxially glabrous corolla lobes.

Metastelma sepium (Decne.) W. D. Stevens, Phytologia 64: 335. 1988. *Vincetoxicum sepium* Decne., in A. P. de Candolle, Prodr. 8: 526. 1844. *Cynanchum sepium* (Decne.) Standl., Contr. U.S. Natl. Herb. 23: 1177. 1924. TYPE: Mexico. Oaxaca: in montibus, 2300 m, *H. G. Galeotti 1533* (holotype, P!; isotypes, G!, K!).

A member of the genus *Orthosia* because of its basally fused corona and adaxially glabrous corolla lobes.

Insufficiently Known Name

Metastelma selerianum Schltr., Bull. Herb. Boissier 6: 841. 1906. TYPE: Mexico. Chiapas: Cerro de Tonalá, "in pratis montanis," Feb., *C. Seler & E. Seler 2056* (holotype, B destroyed).

In contrast to *Metastelma lanceolatum*, no specimen annotated "*Metastelma selerianum*" by Schlechter or anyone else was found, and the description gives no hint as to the identity of the taxon.

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APPENDIX 1. Numerical index of species.

1a. *M. arizonicum* subsp. *arizonicum*
1b. *M. arizonicum* subsp. *chiapense*
2a. *M. barbigerum* var. *barbigerum*
2b. *M. barbigerum* var. *liesnerianum*
2c. *M. barbigerum* var. *veracruzense*
3a. *M. californicum* subsp. *californicum*
3b. *M. californicum* subsp. *lanceolatum*
4. *M. cuneatum*
5. *M. eliasianum*
6. *M. latifolium*
7. *M. longicoronatum*
8. *M. mexicanum*
9. *M. minutiflorum*
10. *M. palmeri*
11. *M. pedunculare*
12. *M. pringlei*
13. *M. schaffneri*
14a. *M. schlechtendalii* var. *schlechtendalii*
14b. *M. schlechtendalii* var. *arenicola*
14c. *M. schlechtendalii* var. *trichophyllum*
15. *M. stenomeres*
16. *M. turneri*

APPENDIX 2. Index to collections examined.

The numbers in parentheses refer to the corresponding species in the text and in the Numerical List of Species presented above in Appendix 1.

Aguilar 124 (14a); Albers et al. 46448 (2a); Andréz Rodriguez & Carranza 1111 (12); Aspra 65 (14c).

Barkelew 217 (3a); Barkley 13360 (2a); Barkley et al. 7155 (2a); Barlow 28/17 (2b); Bennett et al. 646 (12); Bentham s.n. (3a); Berlandier s.n. (14a); Blake 7793 (1b); Boege 862 (3b), 1301 (2c), 1438 (3b); Brandegee s.n. (3a), (4); Breedlove 14010 (2b), 27183 (7), 27820 (14c), 28258 (14c), 28986 (1b), 62261 (3a), 62528 (3a); Breedlove & Raven 13199 (7); Breedlove & Thorne 20658 (14c); Burch 2984 (2c); Burgess 5695 (1a); Burgess & Van Devender 5235 (12), 7661 (3a); Butterwick 78 (14a).

Cabrera & Cortéz 281 (14a); Cabrera & De Cabrera 9505 (14a); Calderón 1271 (14c); Calvert 117 (2a); Carranza & García 1080 (12); Cavender s.n. (2c); Chase 7418 (3b); Chiang et al. 7527A (10), 7550 (10), 7964 (2a), 8161D (2a), 9015f (12), 9274 (12), 9366a (12), 9501 (12), 11387 (12); Conrad 9319 (10); Contreras 532 (2b), 3068 (1b), 3866 (14a), 6602 (14a), 7237 (14a), 7270 (14a), 8466 (2b), 9336 (10); Correll 33825 (12); Correll & Correll 12756 (2a); Correll & Johnston 19695 (2a), 20219 (12); Cowan 3616 (2a); Cowan & Magaña 3270 (2c); Cowan et al. 5359 (2a); Croft 62 (2a); Crutchfield 1125 (2a), 2984 (2a), 3000 (2a).

Daubenmire 406 (2b); Davidse & Brant 32667 (14a);

Davis & Lightowlers 66297 (3a); Dorantes 5270 (2c); Dorr 2359 (10 × 16); Drees et al. 74-15 (1a); Duke 12414 (5); Dwyer 2809 (5), 12774 (2b); Dwyer & Hayden 7540 (5).

Edwards s.n. (2b); Emory 1057 (12); Endress 97-18 (11); Engard & Getz 331 (12); Engard & Gentry 686 (12); Ertter 4906 (2a), 5357 (2a).

Felger 9579 (1a), 9635 (3a), 15588 (1a); Felger & Hamilton 15620 (1a); Felger & Quijada-Mascarenas 91-33 (1a); Felger & Schneider 95-84 (1a); Felger & Zamulio 84-461 (1a), 84-490 (1a); Fernández 4731 (3b); Fernándes & Barkley 14485 (2a); Ferris 8589 (3a); Fishbein 2460 (6), 2759 (4); Fishbein & McMahon 2750 (3a), 2769 (3a); Fishbein et al. 1362 (8), 1448 (8), 1606 (6), 1878 (1a), 1903 (6), 1905 (6); Flügel & Geiseler 7016 (14a); Friedman 015-95 (4), 104-95 (4), 150-95 (4), 199-95 (4), 284-94 (4), 379-94 (14b); Friedrichsthal s.n. (14a); Fryxell 3651 (2a), 3820 (16); Fryxell & Anderson 3617 (3b).

Galeotti 1571 A (3b); Gaumer 539 (2b), 23436 (14a), 24230 (14a); Gentle 1508 (2b), 1755 (15), 2517 (2b); Gentle, P. H. 3417 (15), 3815 (14a), 4190 (15), 8458 (15); Gentry 1098 (1a), 1298 (1a), 2373 (6), 4857 (9), 5184 (13), 5431 (14b), 5479 (13), 5562 (13), 6723 (2a), 7136 (3a), 7438 (3a), 7716 (3a), 14304 (1a), 14466 (1a); Gentry & Engard 23247 (12); Ghiesbreght 664 (1b); Gilman 140 (1a); Ginzbarg 131 (10); Goldberg 76-322 (6); Goodding 116-45 (1a); 208-45 (1a); Gould et al. 2804 (1a); Greenman 386 (2b); Gregg s.n. (2a); Gutiérrez 4632 (2b), 5462 (14a).

Haber 615 (11); Hall 521 (2a); Harmon 4189 (11); Hartweg 601 (11); Hastings & Turner 67-64 (3a); Haynes & Stewart s.n. (3a); Heller 1559 (2a); Henrickson 6100 (12), 6366b (12), 6427 (12), 7891 (12), 11497 (12), 11724 (10), 12070 (12), 12481 (12), 12980b (12), 19138b (12), 19303 (2a), 20400 (12); Henrickson & Lee 17559 (2a); Henrickson & Prigge 15352 (12); Henrickson & Wendt 12028 (12); Hernandez 1534 (16); 1562 (2a), 1917 (12), 1940 (12); Heyde & Lux 3060 (14a), 6348 (14a); Hill 10627 (10); Hinckley 2105 (12), 3106 (12), 3954 (10), 4088 (10); Hinton 17660 (12), 17776 (16), 23343 (12); Hinton et al. 7310 (3b), 19616 (12), 19732 (2a), 24186 (2a), 24258 (2a); Howell 10639 (3a).

Jenkins 93-88 (8); Jímenez 26 17 (11); Johnston, I. M. 8438 (12); Johnston, I. M. & Muller 261 (12), 834 (12), 950 (12); Johnston, M. C. 4369 (10), 5063B (2a); Johnston, M. C. & Graham 4525 (2a), 4674 (2a); Johnston, M. C. et al. 11457A (12), 11991 (10), 12077 (12), 12125B (12).

Keil 4323 (1a); Killip & Smith 14531 (5).

LaBounty et al. 5947 (12); Lavin et al. s.n. (12); Le Roy s.n. (1a); Lehto 24882 (6); Lemus 11 (12); LeSueur 361 (10); 1053 (12); Liede 3242 (2b); Liede & Conrad, J. 2557 (7), 2604 (13), 2610 (2a), 2612 (10), 2613 (10), 2955 (3a), 2961 (13), 2962 (13); Liede & Meve 2500 (2a), 2501 (12); Lindheimer 459 (2a), 992 (2a); Lundell 651 (14a), 3562 (14a), 5517 (12), 6656 (15), 8734 (2a), 16709 (2b), 17022 (2b); Lundell & Lundell 8113 (14a).

MacDougal, T. H 116 (14c); Machuca 7400 (3b); Marsh Jr. 119 (10); 305 (10); Martin s.n. (3a); Martin & McWorther s.n. (6); Martínez 3634 (13), 14284 (14c); Martinez & Luyando F-2295 (2a); Matuda 3765 (2b); McGee 134 (2a); McKellar s.n. (12); McLaughlin & Bowers 2119 (3a); Mendoza & Mérida 2566 (10); Mendraño 1630 (13); Mogensen 1151 (14a); Molina 12851 (1b), 13162 (1b), 13226 (14c), 13243 (14c), 13344 (14c), 13370 (14c), 15672 (14a), 18455 (14c), 18607 (14c), 22438 (14a), 22442 (14a), 23080 (11); Molina & Molina 24843 (11); Moore Jr. & Wood Jr. 4409 (3b), 4259 (3b); Moran 9141 (9); Moser et al. 18152 (1a) ; Mueller, C. H. 2099 (16), 8115 (12); Mueller, C. H. & Mueller, M. T. 188 (16); Müller, F. 1853 (14a).

Neese & Neese 10076 (1a); Nesom et al. 7592 (2a), 5957 (10); Nixon & Cowan 831 (3a).

O'Neill 8659 (2b), 8660 (15).

Palmer 159 (13), 223 (1a), 360 (2a), 626 (1a), 665 (6), 824 (10), 828 (10); Panero & Calzada 4026 (10), 4040 (10); Patterson 6476 (16), 6519 (2a); Pennell 10220 (2a), 10320 (2a), 17729 (3b); Pérez 85 (14c), 125 (14c); Pittier 3539 (5); Pringle 70 (12), 955 (12), 1776 (13), 2749 (13), 2836 (2a), 3138 (3b), 4766 (13), 5626 (13), 6205 (13), 6646 (2a), 6706 (10), 10838 (3b), 11027 (13), 11841 (16), s.n. (1a); Purpus 1259 (13), 2094 (2c, 14a), 2617 (13), 3244 (10), 7273 (1b), 9078 (1b), 9167 (3b), 9169 (1b), 10217 (1b).

Reeves & Pinkava 13075 (12); Reina et al. 96-286 (1a), 97-1087 (6); Reverchon 1558 (2a); Rodríguez 1024 (12); Roe & Roe 1885 (3b); Roe et al. 997 (14c); Rose-Innes & Moon 1218 (12); Russell et al. 11402 (1a), 11584 (1a), 11629 (1a), 12115 (1a).

Salinas 5790 (10); Salinas & Tenorio 3294 (3b); Sanders 9265 (14b); Sauer & Gade 3137b (2b); Saunders 740 (14a); Schaffner 652 (13); Schiede 11 (14a), 159 (14a), 260 (14a); Schipp 674 (15); Shortman 96-27 (1a); Shreve 6468 (3a), 7197 (3a), 8417 (2a × 12), 9312 (3b); Shreve & Tinkham 9694 (12); Skorepa 173 (14b); Skutch 1438 (14a); Small & Wherry 11875 (2a); Smith M124 (2a); Socorro Gonzales 840 (12); Sousa et al. 10929 (14a); Stanford et al. 68 (12), 362 (12), 920 (NY 2341) (16); Steinmann 955 (6), 93-358 (14b), s.n. (6, 8); Steinmann & Varela 972 (1a); Spellenberg & Repass 5353 (8); Stevens 1250 (14a), 1409 (2c); Stevens et al. 2259 (10), 2260 (10); Stewart 466 (12).

Taylor, J. & Taylor, C. 11393 (11), 12532 (2c); Taylor, M. 172 (12); Taylor, R. J. 4251 (11), 4285 (11); Tenorio et al. 7660 (13), 10441 (3a); Tharp, B. C. 248 (2a), 1185 (2a), s.n. (2a); Thomas & Felger 11785 (1a), 11942 (1a); Ton 1548 (14c), 3092 (14c); Tonduz s.n. (Herb. 10130) (11); Torres & Garcia 6656 (10); Tourney s.n. (1a); Tún Ortíz 604 (14a), 1494 (14a); Turner, B. L. s.n. (13); Turner, R. M. & Hastings 64-128 (14b); Turner, R. M. et al. 79-261 (1a); Tyson et al. 3962 (5).

Van Devender & Eiber s.n. (8); Van Devender & Reina 98-1132 (1a); Van Devender & Yetman 94-698 (4); Van Devender et al. 92-121 (3a), 92-133 (4), 93-1253A (4), 93-1265 (4), 93-1284 (4), 93-1310 (1a), 93-65 (1a), 98-1285 (9), 95-1189 (6), 84-29 (1a), s.n. (8); Vilaseñor et al. 1621 (12); Villarreal & Carranza s.n. (16); Villarreal et al. 3115 (2a).

Wagner et al. 4120 (12); Warnock 21851 (12); Wawra 625 (14a); Webster & Webster 119 (2a); Webster & Wilbur 3060 (2a); Wendt et al. 1328 (10); White, D. & Mott 74 (3b); White, S. 3239 (13); Wiggins 7191 (9), 7491 (1a), 15048 (3a), 15085 (3a), 15628 (13); Wilson 11388 (10); Woodson et al. 1263 (5), 1499 (5), 1500 (5); Wright 1676 (2a), 1677 (8), s.n. (2a); Wyatt 1464 (2a); Wynd & Mueller 26 (12), 244 (10).

S. coll. (Herb. Berlandianum) 3198 (2a).

Appendix 3. Index to scientific names.

Astephanus pubescens Greenm. 83
Basistelma angustifolium (Torr.) Bartlett 61
  mexicanum (Brandegee) Bartlett 61
Cynanchum arizonicum (A. Gray) Shinners 39
  barbigerum (Scheele) Shinners 43

barbigerum (Scheele) Shinners var. *breviflorum* Shinners 68
californicum (Benth.) Moran 47
chiapense (A. Gray) Standl. & Steyerm. 42
collinum (S. F. Blake) Standl. & Steyerm. 42
eulaxiflorum Lundell 82
filisepalum (Standl.) L. O. Williams 82
glaberrimum (Woodson) L. O. Williams 82
grayi Shinners 63
infimicola L. O. Williams 54
liesnerianum L. O. Williams 46
longicoronatum L. O. Williams 57
maccartii Shinners var. *latifolium* Turner ex Henrickson 80
maccartii Shinners var. *maccartii* 63
miserum L. O. Williams 83
palmeri (S. Watson) Blake 64
palmeri (S. Watson) Shinners 63
pringlei (A. Gray) Henr. 68
rubens L. O. Williams 83
schlechtendalii (Decne.) Standl. & Steyerm. 73
sepicola (Pittier) L. O. Williams 66
sepium (Decne.) Standl. 83
sonorense Moran 63
stenomeres Standl. & Steyerm. 80
trichophyllum L. O. Williams 77
wigginsii Shinners 61
woodsonianum L. O. Williams 66
Ditassa mexicana Brandegee 49
Jobinia eulaxiflora (Lundell) W. D. Stevens 82
Melinia angustifolia A. Gray 61
mexicana Brandegee 61
Metastelma albiflorum Griseb. 39
albiflorum S. Watson 39
angustifolium Torr. 61
angustifolium Turcz. 82
arizonicum A.Gray 39
arizonicum A.Gray subsp. **arizonicum** 39
arizonicum A.Gray subsp. **chiapense** (A. Gray) Liede & Meve 42
barbigerum Scheele 43
barbigerum Scheele var. **barbigerum** 43
barbigerum Scheele var. **liesnerianum** (L. O. Williams) Liede & Meve 46
barbigerum Scheele var. **veracruzense** Liede & Meve 46
californicum Benth. 47
californicum Benth. subsp. **californicum** 47
californicum Benth. subsp. **lanceolatum** (Schltr.) Liede & Meve 49
chiapense A.Gray 42
collinum S. F. Blake 42
cuneatum Brandegee 52
decipiens Pittier 73
eliasianum Dugand 54
eulaxiflorum (Lundell) Liede 82
filisepalum Standl. 82
glaberrimum Woodson 82
infimicola (L. O. Williams) W. D.Stevens 54
lanceolatum Schltr. 49
latifolium Rose 57
liesnerianum (L. O. Williams) Liede 46
longicoronatum (L. O. Williams) Liede & Meve 57
macropodum Greenm. 64
mexicanum (Brandegee) Fishbein & R. Levin 61
minutiflorum Wiggins 63
miserum (L. O. Williams) W. D. Stevens 83
multiflorum S. Watson 71
palmeri S. Watson 63
parviflorum R. Br. ex Schult. 73
parviflorum Schltdl. 73
pedunculare Decne. 66
pringlei A.Gray 68
pubescens (Greenm.) W. D. Stevens 83
rubens (L. O. Williams) W. D. Stevens 83
schaffneri A.Gray 71
schlechtendalii Decne. 73
schlechtendalii Decne. var. **arenicola** Liede & Meve 77
schlechtendalii Decne. var. **schlechtendalii** 73
schlechtendalii Decne. var. **trichophyllum** (L. O. Williams) Liede & Meve 77
selerianum Schltr. 83
sepicola Pittier 66
sepium (Decne.) W. D. Stevens 83
stenomeres (Standl. & Steyerm.) W. D. Stevens 80
trichophyllum (L. O. Williams) W. D. Stevens 77
turneri Liede & Meve 80
watsonianum Standl. 39
Pattalias angustifolius (Torr.) S. Watson 61
Vincetoxicum sepium Decne. 83

A TAXONOMIC REVISION OF THE *PAEONIA ANOMALA* COMPLEX (PAEONIACEAE)[1]

Hong De-Yuan[2] *and Pan Kai-Yu*[2]

ABSTRACT

Based on field observation, examination of over 350 sheets of exsiccatae, and investigation of all the relevant types, a taxonomic revision of the *Paeonia anomala* complex is presented. Typifications are clarified for *P. anomala*, *P. intermedia*, *P. hybrida*, *P. sinjiangensis*, *P. altaica*, and *P. reitchii*. The identity of three well-known taxa, *P. anomala*, *P. hybrida*, and *P. intermedia*, is also clarified. Two species, *P. anomala* and *P. intermedia*, are recognized, with the circumscription of *P. anomala* emended to include *P. reitchii* as its subspecies. *Paeonia anomala* includes two subspecies: subspecies *anomala* and subspecies *reitchii* with the former distributed in Central Asia, Siberia, and the northeastern European part of Russia, while the latter occurs in China southeast of the Gobi Desert. *Paeonia intermedia* is distributed in Central Asia, but with an isolated locality in Georgia. *Paeonia sinjiangensis* is treated as a synonym of *P. anomala*, and *P. hybrida* Pallas is treated as a synonym of *P. tenuifolia* L. The lectotypes of *Paeonia laciniata*, *Paeonia beresowskii*, and *Paeonia intermedia* are designated here in the present paper.

Key words: *Paeonia*, *Paeonia anomala* complex, *Paeonia hybrida*, *Paeonia intermedia*, Paeoniaceae.

The *Paeonia anomala* L. complex (Paeoniaceae) comprises a group of herbaceous peonies in Central Asia, Siberia, and adjacent northeastern European regions. They are characterized by leaves biternate with leaflets decurrent at the base, leaflets finely segmented, with segments of a lower (the best developed) leaf ranging from 70 to 100 in number and 4–32 mm in width, and by bristles along veins on the upper blade surface. The only species with which it may be confused is *Paeonia tenuifolia* L., but the latter has leaves even more finely segmented, with segments more than 130 in number and 0.5–6 mm in width.

Since the late 1970s, two new species in the *Paeonia anomala* complex have been described from Xinjiang, the Central Asian part of China: *P. sinjiangensis* K. Y. Pan (1979) and *P. altaica* K. M. Dai & T. H. Ying (1990). For a better understanding of the species group in Xinjiang, we made an expedition in 1993 to the Altai and the Tienshan in Xinjiang and found that morphological features of the group in Xinjiang were not consistent with the descriptions by Schipczinsky (1921, 1937) and Gamaulova (1961); Stern's (1946) treatments and nomenclature are different from theirs but do not reflect the reality of the group in Xinjiang, either. Thus, we realized that the *P. anomala* complex needed a comprehensive taxonomic revision and review of the nomenclature. For this purpose, the first author examined all available specimens of this group in the herbaria at BM, HNWP, K, LE, NWTC, PE, SHI, SHMU, TBI, XJBI, XJNU, and XJU (see Appendix 1). In addition, the types of *P. anomala*, *P. hybrida*, *P. intermedia*, and the other six specific and varietal names were examined at LINN (Herbarium of the Linnean Society), BM, K, and PE, respectively.

HISTORICAL REVIEW

Within the *Paeonia anomala* complex the type species, *P. anomala*, was described from Siberia by Linnaeus (1771). Pallas (1789) described three additional species, *P. laciniata* and *P. sibirica* from Siberia, and *P. hybrida* from a plant raised from seeds of *P. tenuifolia* cultivated in the Botanic Garden of the St. Petersburg Academy in Russia. *Paeonia sibirica* Pallas (1789) shares an illustration (tabula) with *P. laciniata*, but does not have a description. In his monograph of *Paeonia*, Anderson (1818) recognized only *P. anomala*, reducing *P. hybrida* as a synonym of *P. tenuifolia* for the first time. De Candolle (1818) recognized *P. anomala*, *P. hybrida*, and *P. laciniata*, but later (1824) treated *P.*

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laciniata as a synonym of *P. anomala*. Meyer (1830) described the fourth species, *P. intermedia*, from the Altai Mountains. Ledebour (1842) cited *P. anomala*, *P. hybrida*, and *P. intermedia*, treating *P. laciniata* as a synonym of *P. anomala*. Trautvetter (1860) recognized only one species, reducing *P. hybrida* as a variety of *P. anomala*, and treating *P. intermedia* as a form of variety *hybrida*. Lynch (1890) cited *P. hybrida* and *P. anomala*, and stated that the former was native to the Caucasus. Huth (1892) adopted the widest species concept of *P. anomala*, which includes four varieties: var. *typica*, var. *hybrida* (= *P. intermedia*), var. *nudicarpa*, and var. *emodi* (= *P. emodi*, confined to the western Himalayas). A further treatment by Krylov (1901) divided the complex into two species, *P. anomala* and *P. hybrida*, and reduced *P. intermedia* as a variety of the latter, *P. hybrida* var. *intermedia* (C. A. Meyer) Krylov, in addition to the typical variety. In the area of West Tienshan (Kirghizia and Xinjiang, China), Trautvetter (1904) enumerated only *P. anomala*, treating *P. intermedia* as its subspecies. Schipczinsky (1921) basically followed Krylov (1901), recognizing two species, *P. anomala* (with two varieties, var. *anomala* and var. *nudicarpa*) and *P. hybrida* (with two varieties, var. *hybrida* and var. *intermedia*), and the same treatment was adopted for the Flora of the USSR (Schipczinsky, 1937). These two *Paeonia* species were grouped by him as series 4, *Dentatae* Kom. (Schipczinsky, 1937: 33, "leaf lobes incised or with dentate margin"). Roots of both species were described as tuberous. In contrast, Stern (1946) recognized only one species in his monograph of *Paeonia*, *P. anomala*, in which two varieties were recognized: variety *anomala* with glabrous carpels, and variety *intermedia* with tomentose carpels. He did not mention roots of this group. Stern (1946: 113) considered *P. hybrida* Pallas as an ambiguous name: "It is doubtful what species Pallas intended by this name and, as it is not possible to discover what he meant, this name of *P. hybrida* has been omitted." However, in the *Flora of Kazakhstan*, Gamaulova (1961), following Krylov (1901) and Schipczinsky (1921, 1937), described two species, and still recognized *P. hybrida* as a valid name.

While working on *Paeonia* for the *Flora Reipublicae Popularis Sinicae*, Pan (1979) found a specimen from Xinjiang whose roots were basipetally attenuate. According to Schipczinsky (1937) and Gamaulova (1961), *Paeonia anomala* and *P. hybrida* have tuberous or fusiform roots, so the plant was described by her as a new species, *P. sinjiangensis* K. Y. Pan; the plants with tuberous or fusiform roots were treated as *P. anomala* with two varieties: variety *anomala* and variety *intermedia* (Pan, 1979). Also from Xinjiang, Dai and Ying (1990) described another new species, *P. altaica*, which was stated to have flowers larger than *P. sinjiangensis* and one or two underdeveloped flower buds in addition to the terminal blooming flower.

Interestingly, Schmitt (1999) failed to recognize the distinct differences between *Paeonia anomala* and *P. intermedia* in the root and calyx, and thus treated them as a single species, but still recognized *P. sinjiangensis* and *P. altaica* as distinct species.

From the above it is clear that *Paeonia hybrida*, *P. intermedia*, and *P. anomala* have been variously treated. With this paper we hope to clarify the biological attributes and variations of the *P. anomala* complex.

Observations and Discussion

To answer how many species were really present in Xinjiang and what biological features they have, the first author and coworkers (Hong et al., 1994) made an expedition to the Tienshan and Altai Mountains, conducting field observations and population samplings of *Paeonia* in 1993. Seven populations in total were observed, covering those character states previously described for the *P. anomala* complex (Table 1). We found there were only two species in Xinjiang that differed distinctly from each other in the root and calyx. One species had the roots basipetally attenuate (carrot-shaped) and sepals mostly caudate (Fig. 2), preferring relatively moist habitats in woods. This was treated as *P. sinjiangensis*. The other had roots tuberous or fusiform and sepals mostly (at least 2) rounded but not caudate at apex, growing on sunny, shrubby or grassy slopes, or in sparse woods. This latter was recognized as *P. anomala*. We also found the presence or absence of indumentum on the carpels in this species group to be a polymorphism, i.e., individuals with carpels either glabrous or from sparsely to densely pubescent could be found within a single population (Table 1). The indumentum on carpels was demonstrated as quite variable, although it was considered by the previous authors as taxonomically valuable. Therefore, any taxonomic division based on this character, such as that between *P. anomala* and *P. anomala* var. *nudicarpa* (by Huth, 1892) or *P. anomala* and *P. anomala* var. *intermedia* (by Stern, 1946), is artificial. Also not observed by the previous authors was the clear differentiation in root and calyx in this group, which are closely correlated with each other (Fig. 2).

We also found that in the form with carrot-shaped

Table 1. The populations sampled and their characters in the *Paeonia anomala* complex in Xinjiang, China (all the vouchers are in PE). The figures before parentheses indicate character states, while those in parentheses indicate the number of individuals observed. The indumentum on carpels is divided more or less arbitrarily into six grades with "0" expressing totally glabrous, "1" extremely sparsely hairy, "5" entirely covered with hairs, while "2," "3," and "4" are in between.

Population	Locality and habitat	Roots	Leaf color	Number of non-caudate sepals	Indumentum on carpels
D. Y. Hong et al. 3	Altai: Mt. Halamaryi, NW of Altay City, 1200 m, *Populus* forest by stream	carrot-shaped (3)	pale green	0(2); 1(3)	0(2); 1(1); 5(1)
D. Y. Hong et al. 5	Altai: Xiaodong Gou Valley, NE of Altay City, 1060 m, *Populus-Betula-Picea* forest at valley bottom	carrot-shaped (3)	pale green	0(2)	0(1)
T. H. Ying 1006–1022	Altai: Habahe County, 1200–1550 m, in *Betula* forests	carrot-shaped (2)		0(4); 1(1)	5(4); 0(2)
D. Y. Hong et al. 2	Altai: Mt. Halamaryi NW of Altay City, 1300 m, S slope, rocky *Berberis-Spiraea* bushes	fusiform to tuberous (3)	green	2(1); 3(5)	0(1); 2(1); 3(5)
D. Y. Hong et al. 0125	Altai: Mt. Halamaryi, NW of Altay City, 1000 m, sparse bushes	fusiform to tuberous (2)	green	2(1); 3(2)	0(2); 5(1)
D. Y. Hong et al. 4	Altai: Xiaodong Gou, NE of Altay City, 1060 m, W slope, rocky sparse *Spiraea-Berberis* bushes	fusiform to tuberous (6)	green	3(2); 4(1)	0(1); 5(3)
D. Y. Hong et al. 1	Tienshan: Yining County, Yining Forest Farm, 1150–1200 m, N slope, sparse *Prunus-Malus* forest with *Cotoneaster* & *Spiraea*	fusiform to tuberous (5)	green	2(4); 3(1)	5(5)

roots, the petals varied greatly in length, from 3.5 to 6.5 cm, and in the Altai Mountains some individuals of this form possessed one or two additional underdeveloped flower buds similar to *Paeonia veitchii*. This was again a polymorphism, and not considered by us to be a stable character, and therefore *P. altaica* was reduced to a synonym of *P. sinjiangensis* (Hong et al., 1994).

After examination of about 200 sheets of herbarium specimens in the Komarov Institute of Botany (LE) in 1999, the first author found that two species could also be distinguished in this complex: one with the roots carrot-shaped and sepals mostly caudate, while the other with the roots tuberous or fusiform, and sepals mostly non-caudate. These biological features match those on plants observed in Xinjiang (Hong et al., 1994). Gamaulova (1961, tab. 2) described roots of *Paeonia anomala* as fusiform-thickened, and those of *P. hybrida* as tuberous-thickened. However, roots of *P. intermedia* (= *P. hybrida* sensu Schipczinsky and Gamaulova) vary in shape from tuberous consistently to fusiform, and this variation could be found within populations or even on the same individual, whereas in *P. anomala* neither fusiform-thickening nor tuberous-thickening were found.

Contradictions exist between our natural observations (Hong et al., 1994) and earlier descriptions by Schipczinsky (1937) and Gamaulova (1961). Stern's (1946) treatment of this complex as one species with two varieties (*P. anomala* and *P. anomala* var. *intermedia*) is also at variance. For a clear taxonomic revision and correct nomenclature, one remaining issue ought to be resolved: the identity of *Paeonia anomala, P. hybrida,* and *P. intermedia.* The type specimen of *P. anomala,* with two visible sepals both caudate and relatively thin leaves, is perfectly consistent with the form with carrot-shaped roots. According to the type specimen at LINN [Siberia, no. 692. 3], field observation, and examination of over 350 sheets of exsiccatae, *P. sinjiangensis* and *P. altaica* should be treated as synonyms of *P. anomala*; the descriptions of roots of *P. anomala* by Schipczinsky (1937) and Gamaulova (1961) are erroneous. The type of *P. hybrida* (at BM), on which Pallas's (1789) tab. 86 was apparently based, has leaf segments 3–4 mm in width, and at least more than 100 in number, and is thus within the range of variation in *P. tenuifolia* L. (Hong & Zhou, 2003). Therefore, *P. hybrida* Pallas should be treated as a synonym of *P. tenuifolia*, as Anderson (1818) suggested nearly 200 years ago. The type specimen of *P. intermedia* at K possesses tuberous roots, mostly non-caudate sepals, and relatively thick and narrow leaf segments. The plants

that have tuberous or fusiform roots, are distributed widely from the Altai to Tadzhikistan and Uzbekistan, and were named *P. hybrida* by Schipczinsky (1921, 1937) and Gamaulova (1961) correspond to this type specimen very well.

Stern's (1946) statement concerning the name of *Paeonia hybrida* is not correct, confusing *P. intermedia* with *P. anomala*. Pan's (1979) treatment of the *P. anomala* complex (a new species, *P. sinjiangensis*, and *P. anomala* with var. *intermedia*) is also unjustifiable. Although Hong and his coworkers (Hong et al., 1994) properly described two species and clearly stated their morphological and ecological differences for this group, the nomenclature they used is misapplied.

The *Paeonia anomala* complex comprises two species: *P. anomala* and *P. intermedia*. *Paeonia emodi*, which was treated as a variety of *P. anomala* by Huth (1892), remains a distinct species, with leaves ternate, without bristles on the upper surface, leaflets much less segmented, segments no more than 40 in number and 1.5–4 cm wide, carpels usually two, less frequently one, very rarely three, and flowers white. *Paeonia veitchii* Lynch was described from Sichuan Province, China (Lynch, 1890), and was said (Stern, 1946; Pan, 1979) to differ from the *P. anomala* group in having several flowers instead of a single flower on a stem. According to our observation, one or two underdeveloped flower buds sometimes also exist in addition to one normal and terminal flower in *P. anomala*, while *P. veitchii* sometimes has flowers solitary (*P. veitchii* var. *uniflora*), although it has 3 or 4 flowers or 1 to 3 underdeveloped flower buds in addition to the terminal flower on a stem. Thus, *P. veitchii* was reduced to a subspecies of *P. anomala* (Hong et al., 2001).

KEY TO THE *PAEONIA ANOMALA* COMPLEX

1a. Roots carrot-shaped, never tuberous or fusiform; sepals all or mostly caudate, less frequently one or very rarely two non-caudate ..... 1. *P. anomala*
  2a. Flowers solitary, rarely 1 or 2 underdeveloped flower buds present in addition to terminal flower on a stem ..... 1a. *P. anomala* subsp. *anomala*
  2b. Flowers usually 2 to 4 on a stem or 1 to 3 underdeveloped flower buds present in addition to terminal flower, rarely flowers solitary on a stem ..... 1b. *P. anomala* subsp. *veitchii*
1b. Roots fusiform or tuberous; inner 2 to 4 sepals rounded but non-caudate at apex ..... 2. *P. intermedia*

TAXONOMIC TREATMENT

1. Paeonia anomala L., Mant. 2: 247. 1771. TYPE: Siberia, no. 692.3 (holotype, LINN!). Figure 1A.

Paeonia laciniata Pallas, Fl. Ross. 1(2): 93, tab. 85, sub *P. sibirica*, 1789. TYPE: the illustration (tab.) cited in the protologue (lectotype, designated here!).
Paeonia sibirica Pallas, Fl. Ross. 1(2): tab. 85. 1789.

Pallas's (1789) illustration (tab.) 85 has only one name, *P. sibirica*, and apparently he used this illustration also for *P. laciniata* because one sees "*Paeonia laciniata* Tab. LXXXV" on p. 93. *Paeonia laciniata* was described in detail by Pallas, but no description of *P. sibirica* was given by him.

Perennials; tap roots ≥ 50 cm long, carrot-shaped, basipetally attenuate, up to 2 cm diam., lateral roots slender, neither tuberous nor fusiform. Leaves biternate; leaflets finely segmented; lower leaves with segments 70 to 100 in number, 8–32 mm in width. Flowers solitary or 2 to 4 on a stem, often only terminal one fully developed and blooming; sepals 3 to 5, mostly caudate at apex, rarely 1 or very occasionally 2 non-caudate; carpels 2 to 5, from glabrous to densely tomentose.

The species prefers relatively moist habitats, growing in forests, on the edges of forests, or rarely in bushes. It is found at altitudes from 1100 to 3870 m.

This species is widely distributed from central China to the Kola Peninsula of Russia via Siberia and Central Asia. The species is of two allopatric subspecies, with the typical subspecies distributed northwest of the Gobi Desert, while subspecies *veitchii* is in China southeast of the Gobi Desert (Fig. 3).

1a. **Paeonia anomala** subsp. **anomala**

Paeonia sinjiangensis K. Y. Pan, Fl. Reipubl. Popularis Sin. 27: 603, fig. 12. 1979. TYPE: China. Xinjiang: Habahe County, *Larix* forests, 1973, *Y. R. Ling 1141* (holotype, PE!).
Paeonia altaica K. M. Dai & T. H. Ying, Bull. Bot. Res. (Harbin) 10(4): 33, fig. 1. 1990. TYPE: China. Xinjiang: Habahe County, Wuzliti, 1550 m, in forests, 10 June 1980, *T. H. Ying 1007* (holotype, SHMU; isotype, PE!).

The typical subspecies is usually found in deciduous or conifer forests, in valleys, less frequently in meadows, at altitudes from 1100 to 2200 m. Apparently it prefers relatively moist habitats. This subspecies is of very wide distribution: northeast Kazakhstan, northern Mongolia, from the Altai and Baikal to the Kola Peninsula in Russia, and in the Altai and adjacent regions in Xinjiang, China (Fig. 3).

Additional specimens examined. CHINA. **Xinjiang:** Altay, *L. R. Xu s.n.* (PE); Mt. Halamaryi, *D. Y. Hong et al. Population No. 3* (PE), *0128* (PE); Xiaodong Gou valley, *T. H. Ying 1001* (PE, SHMU). Burqin: Kem, *N. R. Cui 86624* (XJNU). Emin: Shiyue Township, Wuerkehe'er,

Figure 1. *Paeonia* holotype specimens: —A. *P. anomala* (LINN). —B. *P. hybrida* Pallas (BM). —C. *P. intermedia* C. A. Meyer (K): the insert at upper right is the enlargement of the label at lower right.

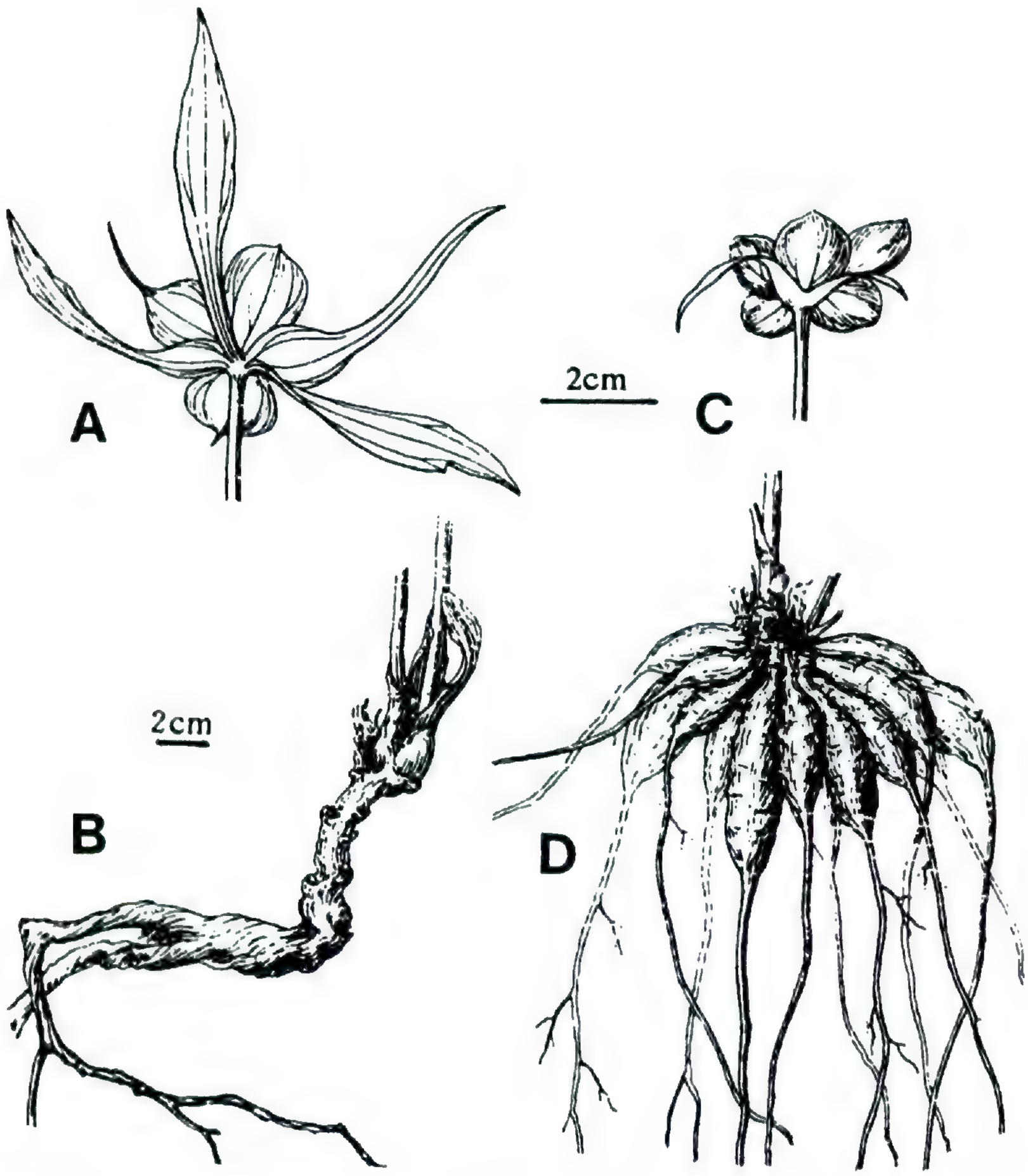

Figure 2. Diagnostic features of *Paeonia anomala* (A, B) and *P. intermedia* (C, D). Tuberous or fusiform roots are correlated with non-caudate sepals, while carrot-shaped roots correlated with usually caudate sepals.

right bank of Telikete River, *Xinjiang Branch Acad. Sinica 012* (XJBI). Fuhai: Ahebai, glades, *s. coll. 3867* (XJBI); Daqiao Forest Farm, *T. H. Ying 1011* (PE, SHMU). Fuyun: *C. W. Chang 11356* (XJBI). Habahe: Baihaba, *Z. M. Mao 10413* (XJBI); Tielieke, Zamanashi Valley, *C. W. Chang et al. 10255* (XJBI); Tiekeliti, *T. H. Ying 1010* (PE, SHMU); Wuzlity, *T. H. Ying 1022* (PE, SHMU). Jeminay: Xingfu Township, Sanxie Valley, *Integ. Exped. 7305* (XJBI). Qinghe: Daqinghe, Mudeng Valley, *Integr. Exped. 11829* (XJBI). Tacheng: Mt. Ba'erleike, *X. Y. Li 870147* (SHI). Toli: Jiayi'er Gold Mine, *N. R. Cui 091* (XJNU); Mt. Zayier, N slopes, *Integr. Exped. (Biology) 630* (XJBI). Wenquan: A'erxiaoto Gou, *F. M. Zhang 90-346* (XJNU). Yumin: Ku'erzhai, *Liu & Shen 8308* (XJBI). KAZAKHSTAN. **Semipalatinsk Province:** Altai, near Altaiskaya Station, Mt. Narymsky region, gorge slopes, *Ladygin 92* (LE). Southern Altai: Mt. Ivanovsky Range, near Gorno-Ulbinki, *I. Rohderi s.n.* (LE). Ustkamenogorsk region: Mt. Altai, Kunduzda River valley, *V. & A. Reznichenko 360* (LE); Mt. Kalbinskie, Saryshbay River valley, *V. Reznichenko 49* (LE); Mt. Kalbinskie, Ulansky, near Asybulak, by Tainta River, *P. Yurchenko s.n.* (LE); Mt. Narymsky, upper Urkar River, *V. Reznichenko 58* (LE); near Ulbinsky gorge, *V. Iljin s.n.* (LE); Urunhaika River mouth, S banks of Marka-Kul Lake, *A. Sedelnikov s.n.* (LE). Zaisan region: Mt. Altai, Ulkunchumek River valley, upper Kaldzhir River, *V. Reznichenko 106* (LE); Markakul Lake, *B. Keller s.n.* (LE); Mt. Narymsky Range, Ak-tui River valley, *D. Yakovlev 69* (LE); Mt. Saur, Chagan-obo River valley, *V. Reznichenko s.n.* (LE); Mt. Saurkie, Maly Dgewen River valley, *B. Keller s.n.* (LE). MONGOLIA. **Ulan Bator:** 10 mi. E of Ulan Bator, *P. Morgan 23* (K). **Gloucester:** Mongolia–Chinese Turkestan Exped. *M. P. Price 293* (K). **North Mongolia:** Mt. Saldzharsky Pass, *E. Klements 11a* (LE). RUSSIA. **Altai Region:** Altai: between Charga & Shabolina, mtn. slopes, *E. K. Klements 4d* (LE); Chuja road, Saadak-lary, *Vereshagin 296* (LE). West Altai: Mt. Listvennitchny, near Nizhne-Uimonskoye, *S. Kolomoitseva 236* (LE). **Buryato-Mongolian Autonomous State:** Baikal, Tunkam, *Turczaninow s.n.* (LE); Zabaikalje, upper Toreika River, 130 km W of Troitskosavsk, *P. Mihno s.n.* (LE). **Eubinsk Region:** West Sayan, Mt. Alan Range, Golets Taskalyk, *I. Krasnoborov 6765* (LE); near Buiba Station, by river, *Krasnoborov & Sannikova s.n.* (LE). Tuva: Tandinsky distr., East Mt. Tannudla Range, near Shurmak, *V. Hanminchun 515* (LE); Ulug-Hemsky distr., Uiuksky Mtn. Range, Bajan-Kol River valley, Orto-Hem tributary, *Lomonosova & Ivanova 89* (LE). **Irkutsk Region:** Irkutsk Prov.: Lena River valley, upper Gulm River, *I. Kuznetsov 114* (LE). Balagansky distr.: near Bazheevskoye, *N. Maltsev 79* (LE). Nizhneudinsky distr.: by Angara River, opposite Yandov, *S. Ganeshin s.n.* (LE); Mt. Hariba-bim Range, Angara River valley, Karpovskoye, *A. Korovkin 290* (LE); by Oka River, *A. Krishtofowich s.n.* (LE); near

Vidimka, Vidim River, *S. Kucherovskaya 282* (LE). Tunkin distr.: Mt. Sayany, near Nylova Pustyn, *V. Komarov s.n.* (LE); Nizhnaya Tunguska valley, near Nizhnaya Korelina, *S. Kokulin 254* (LE). Tunkinsky distr.: Kuren Arshan, *V. Smirnov s.n.* (LE). Verholensky distr.: Biriulka, near Yushina, *P. Alexandrov 179* (LE); Harat, *G. Dolenko 108* (LE); Lena River & Kirenga valley, Toptykan, *M. Tomin 67* (LE); Tutura, *P. Alexandrov 219* (LE). **Kola Peninsula:** Ponoi River, left bank, 8 km from its mouth, *E. Chernov 3* (LE); Ponoi River, near its mouth, *N. Orlova 240* (LE). **Krasnoyarsk Region:** Belsk distr.: near Alshat, *I. Kuznetsov 4661* (LE); Chadobets, *G. Borowikow s.n.* (LE); Rybnoe, *Dranitsyn & Kochubei s.n.* (LE). Enisei Prov., Achinsk distr.: near Ingol Lake, *A. Suhareva s.n.* (LE); near Maloye Lake, *M. Ermolajeva s.n.* (LE); Bolshe-Uluiskaya, near Bobrovki, *I. Kuznetsov 53* (LE); Chuksha River Valley, *I. Tolmatschew 247* (LE); Katanga, *G. Borovikov s.n.* (LE); Vyezzhi Log, *A. Tugarinov s.n.* (LE). Kansk distr.: Gutar River valley, by Kamenka tributary, *W. Troitsky s.n.* (LE); near Kansk, *A. Shliahtin s.n.* (LE); Rybnaya River valley, Perovskoye, *I. Kuznetsov 193* (LE); near Nazimovskoye, *Z. Evseeva 4406* (LE). Krasnoyarsk Prov.: Chunia River, right bank opposite mouth of Mutorai River, *A. Rubin s.n.* (LE); Hakassia, Shirinsky distr. Bolshaya Iiusa River valley, NW slopes, *Polozhii & Kandasova s.n.* (LE); near Krasnoyarsk, by Mohovaya River, *V. Verhovskaya & M. Mishin 104* (LE); Minusinsk, Bolshoye Kysylkul Lake, *K. Golubeva et al. s.n.* (LE); Nizhnaya Tunguska River valley, near mouth of Hurkakit River, *Rubin & Maskil s.n.* (LE); between Salba & Grigorievka, *P. Krylov s.n.* (LE); Shushensky distr. near Tanzyben, by Black Tanzyben River, *Kuminova & Alexeeva s.n.* (LE); near Sorokino Station, N slopes, *Cherepnin s.n.* (LE). **Novosiberia Region:** Altai: Elikmanar, upper Karakol River, *V. Vereshagin 345* (LE). Kuznetsky Alatau: Kondoma River valley, Kazany Mine, Mt. Kyon, *B. Klopotov s.n.* (LE); upper Sary-Chumysh River, near Ulus Munai, *A. Vydrin s.n.* (LE); Tom River valley, Mt. Tohpan-taiga, *B. Klopotov s.n.* (LE). Mariinsky Prov.: Biisk, Black Anuj, Talitskiebelky, to Kazanda, *Pobedimova 697* (LE); Biisk, Lebed River valley, by Chuja River, *B. Klopotov 180* (LE); Biisk, between Tulatinskaya & Sentelek, *N. Kuznetsov 1991* (LE); Kainsk, Verhnyaya Nazarova, *B. Klopotov 113* (LE); Narym, Ixa River, *S. Genina s.n.* (LE); Sofronova, *P. Krylov s.n.* (LE); Tomsk distr.: Chulym & Chet River valley, *P. Sokolov 13a* (LE). Moshkovsky Prov. (Distr.): Uskorniha River valley, *Kuvajev & Sabitov s.n.* (LE). Toguchinsky distr., near Mirny, *Lashinsky & Ronginskaya 973* (LE). **Omsk Region:** Tobolsk Province: Berezov distr., Lopsia River, tributary of Severnaya Sosva, *s. coll. s.n.* (LE); Tobolsk distr., Landinka River valley, *E. Vislouh 73* (LE). **Ural:** Arctic Ural: Lyapin tributary, upper Manja River, *V. Sochava 100* (LE); Severnaya Sosva River valley, Lyapin tributary, upper Khulga River, *B. Gorodkov 512* (LE). Marriinsky distr., Beket River valley, Kolsonskoye, *N. Kuznetsov 199* (LE). Tobolsk Province: Berezovsky distr., Berezov, *Pohle & Rozhdestvensky s.n.* (LE); Tarsky distr., Rybinsk, near Pustynnoye, *V. Varentsov s.n.* (LE). **Yakutsk Autonomous State:** Yakutia, Suntarsky distr., upper Vilyuy River, Tuoikhaia, by Chona River, *I. Kildushewsky 150/22* (LE).

1b. Paeonia anomala subsp. **veitchii** (Lynch) D. Y. Hong & K. Y. Pan, Novon 11: 317. 2001. *Paeonia veitchii* Lynch, Gard. Chron. ser. 3, 46: 2 tab. 1. 1909. TYPE: China. W. Sichuan: Tatien-lu (Kangding), 8–10,000 ft., *E. H. Wilson* (for *James Veitch & Sons*) *3034* (holotype, K!, photo, PE!).

Paeonia beresowskii Komarov, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 5. 15 Jan. 1921. *Paeonia veitchii* var. *beresowskii* (Komarov) Schipczinsky, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 2: 46. 26 Mar. 1921. TYPE: "China Occid, Szechuan (Sichuan), Sun-pan-tin (Songpan), Guichua," 9 June 1894, *M. Beresowskii s.n.* (lectotype, designated here, LE not seen).

Paeonia veitchii var. *woodwardii* (Stapf ex Cox) Stern, J. Roy. Hort. Soc. 68: 130. 1943. *Paeonia woodwardii* Stapf ex Cox, Pl. Introd. Farrer 43. 1930. TYPE: China. Gansu: Zone (Chuoni), *R. Farrer 67* (holotype, E not seen).

Paeonia veitchii var. *leiocarpa* W. T. Wang & S. H. Wang, Fl. Reipubl. Popularis Sin. 27: 603. 1979. TYPE: China. Sichuan: Jinchuan, Kasa Township, Yinchanggou, forests by stream, 2700 m, 26 Apr. 1958, *X. Li 77248* (holotype, PE!).

Paeonia veitchii var. *uniflora* K. Y. Pan, Fl. Reipubl. Popularis Sin. 27: 603. 1979. TYPE: China. Sichuan: Gaze, Xiongjiling, 3600 m, mtn. summit, bushes, 18 June 1974, *Qinghai-Xizang Exped. Veget. Group 034* (holotype, PE!).

This subspecies, though distantly isolated from *Paeonia anomala* subsp. *anomala* by the huge deserts of the Gobi, still very much resembles the latter. The only remarkable difference between them is the number of flowers on a stem. *Paeonia anomala* subsp. *veitchii* usually possesses 2 to 4 blooming flowers in addition to up to 2 underdeveloped flower buds. Very rarely only the terminal flower blooms in addition to up to 3 flower buds. *Paeonia anomala* subsp. *anomala* possesses only a single terminal blooming flower, without or infrequently with 1 to 3 underdeveloped flower buds.

The subspecies is widely distributed in China: southeastern and central Gansu, southern Ningxia, eastern Qinghai, the Qinling Range of Shaanxi, Shanxi, western Sichuan, and the eastern extreme of Xizang (Tibet) (Fig. 3). Like subspecies *anomala*, *Paeonia anomala* subsp. *veitchii* prefers relatively moist habitats, growing in forests, grasses on the edges of forests, bushes, or subalpine and alpine meadows with shrubs, at altitudes from 1800 to 3870 m.

Phenology. The subspecies flowers from late April to early June, and fruits in August and September.

Chromosomes. $2n = 10$ (Hong et al., 1988).

Additional specimens examined. CHINA. **Gansu:** Dingxi, *s. coll. s.n.* (CPB). Hezheng: Xinzuang, *Gansu Herbs Group s.n.* (NWTC). Hezuo: Mt. Dalinke, *Q. R. Wang 7034* (NWTC). Jiangcha: *S. Gansu Grassland Exped. 681* (NWTC). Kangle: Mt. Taizi, *G. L. Zhu 80006* (NWTC); Mt. Lianhua, *M. S. Yan 1843* (NWTC). Kangxian: s. loco,

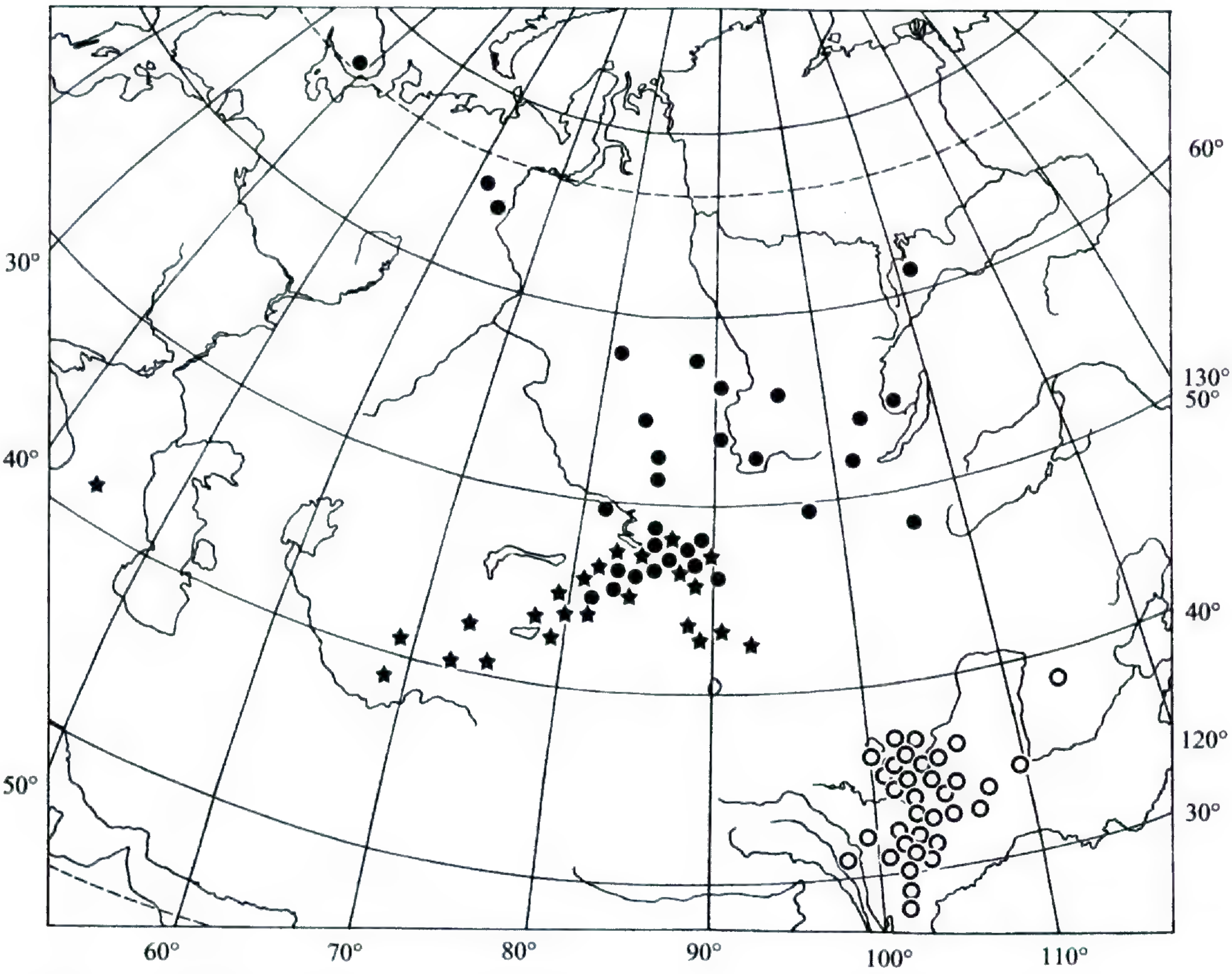

Figure 3. Distribution map of the *Paeonia anomala* species complex. Black circles: *Paeonia anomala* subsp. *anomala*; white circles: *P. anomala* subsp. *veitchii*; stars: *P. intermedia*. Each site in the map is supported by a single or several vouchers cited in the text.

s. coll. s.n. (NWTC). Lanzhou: Mt. Xinlong, *s. coll. 84* (NWTC); Mt. Tiandu, *s. coll. s.n.* (NWTC). Linxia: near Senanpa, by river, *T. K. Fu 834* (PE). Longdie: Dacaopo, *H. J. Zhou 708* (NWTC). Minxian: Lujing, Zhongchuangou, *J. Q. Wang 197* (NWTC); Mt. Luodadoujidela, *T. P. Wang 15240* (PE); near Mawu, *T. P. Wang 4594* (PE); between Lintao and Yuzhong, *Huanghe Exped. 1689* (PE); Mt. Wutai, *Taohe Exped. 3243* (PE); Lamathan, *K. S. Hao 604* (PE). Taohe: *J. F. Rock 12829* (PE). Tsaluku to Shimen, *J. F. Rock 13127* (PE). Tianshui: Mt. Xinjia, *W. Y. Hsia 5707* (PE). Tianzhu: Anyuan, *Y. Q. He 4516* (PE); Zhucha, *Y. Q. He 4915* (PE); Jinqiang Township, Mt. Maomao, *Q. R. Wang 1869* (NWTC). Xiahe: Chingshui, *T. P. Wang 6944* (PE); Tangar'ang, Longwagou, *Q. R. Wang 7270* (NWTC). Yongdeng: Liancheng, Tulugou, *J. L. Bai 8613* (NWTC). Yuzhong: Xinlong, near Yangdaowan, *s. coll. s.n.* (PE). Zhangxian: Caotan distr., *Huanghe Exped. 03183* (PE); Mt. Guiqing, *Huanghe Exped. 4735* (PE); Hediling, Mt. Kehu, *Huanghe Exped. 4655* (PE); Shichuan Forest Farm, Jinhuachi, Lian, *Wang et al. 79197* (NWTC). Zhouqu: Taozhou Forest Farm, *Jiang & Jin 00386* (PE). Zone (Chuoni): Kache Forest Farm, *Lian & Chen 31* (NWTC); Wanchang, Sangtanagou, *Lian & Chen 72* (NWTC). **Ningxia:** the Liupan Mountain Range, *Y. W. Cui 10281* (PE). **Qinghai:** Datong: Kuanghuizu, *K. M. Liou 6019* (PE); near Anchiapu, *K. M. Liou 5970* (PE); Dongxia, *Yu, Lu, Gu & Li 68* (PE); Mt. Laoye, *Liang et al. 378* (HNWP); Baoku, *Z. H. Zhang et al. 4291* (HNWP). Huangyuan: Mt. Banjie, *P. C. Tsoong 8842* (PE). Huangzhong: Sanhei Forest Farm, *S. X. Wang 1065* (HNWP); 40 km W of Xining, *S. X. Zhen 0351* (PE). Huzhu: Beishan Forest Farm, *Guo & He 9012* (HNWP); Qiaotou, *Guo & Wang 6717* (HNWP). Jainca: near Angla, *Liu & Luo 1040* (HNWP). Ledu: Maying Township, Kongjiazui, *B. Z. Guo 6767* (HNWP). Golog: Markog Forest Farm, Hongjungou, *W. Y. Wang 26818* (HNWP). Menyuan: Semnyi, betw. Lihua & Dalong, *Z. Y. Qing 1218* (HNWP, PE); Semnyi, Zhugusi, Xielong, *B. Z. Guo 7396* (HNWP); Semnyi, Hankegou, *Gansu-Qinghai Exped. 2493* (PE). Minhe: Gushan, Nanxia, *L. H. Zhou 2528* (HNWP); Xin'erbeishan, *B. Z. Guo 7010* (HNWP). Tongren: Rongwo, *B. Z. Guo 10232* (HNWP); Shuangfengxi, *B. Z. Guo 10186* (HNWP). Xining [Sining]: Shangwuchuang, *K. S. Hao 779* (PE). Xunhua: Mengda Forest Farm, *Guo & Wang 25058* (HNWP); Mt. Dalijia, *G. Z. Zhang 005* (HNWP). **Shaanxi:** Huxian: Taipingyu, Hualingwan, *Pharmac. Exped. 2019* (PE). Hwainhsien [Huayin]: Qinglongbei, *W. Y. Hsia 4539* (PE). Mt. Taibai: near Dadian temple, *W. Y. Hsia 4571* (PE); Sanchaixia, *K. J. Fu 4441* (PE); Dadian temple to Dumugong temple, *Hong & Zhu PB85065* (PE). **Shanxi:** Shiziping, Xigou, *Shanxi Exped. Wang & Tian 594* (PE). Mt. Wutai: Xitai, Xiachantan village, Xiejiagou, *Shanxi Exped. 684* (PE). **Sichuan:** Baoxing: Raozhi, Nibagou, *Hong & Zhong PB82105* (PE);

Longdong distr., Zhonggan, Mt. Daping, *Sichuan-Econom. A59-0246* (PE); Ganyanggou, *T. T. Yu 2200* (PE); Dengchigou, *T. H. Tu 4329* (PE); Lianghekou, Mahuangpo, *Zhang & Ren 5572* (PE). Barkam: near Puyajiao, *X. Li 71029* (PE); near Kanzhugou, by river, *X. Li 70441* (PE); Pu'ermagou, 209 Lumbering Ground, *X. Li 70867* (PE); Bu'ermagou, *X. Li 70903* (PE); near Matan, *X. Li 71645* (PE); Dalongjiaogou, *X. Li 70685* (PE); near Kafeiqiao, *X. Li 71196* (PE); Zonggag, *X. Li 70719* (PE); Nazhugou, *X. Li 71087* (PE). Emei: Jieyindian, *T. H. Tu 362* (PE). Dege: *S. X. Jia 229* (PE). Garze: S bank of Yalongjia River, *Y. W. Cui 4348* (PE). Heishui: Shidiaolou Township, *Sichuan-Econom. A59-1208* (PE); Sandougou, *Sichuan-Econom. A59-1001* (PE). Jinchuan: Zosijia, *P. X. Li 10137* (PE). Jiulong: Mt. Baitai, between Niupo & Baitai village, *J. S. Ying 3869* (PE). Kangding: Yulingong, Yingbapo, *Hu & He 10463* (PE); Yulin Township, Simaqiao, *Jiang & Yiong 35625* (PE); Yulin Township, Laoyulin, *X. C. Jiang 36014* (PE); Taiyangshan distr., *Hu & He 10373* (PE); Niugu village, *W. Sichuan Exped. Kuan et al. 243* (PE); Xinduqiao, *W. Sichuan Exped. Kuan et al. 732* (PE); Shade distr., Mi'Along, *Nanshui-Beidiao Exped. 02912* (PE); Zhonggu village, Dagaigou, *W. Sichuan Exped. Kuan et al. 352* (PE); between Kangding & Dawu, *P. C. Tsoong 5004* (PE). Lixian: Longxi, Yiduo village, *Z. He 12339* (PE); Miyaluo, Misugou, *S. Jiang A-7162* (PE); Shuanjingsi, *P. X. Li 10100* (PE); Shuanjingsi, 333 km milestone of Chengdu–Aba highway, *Zhang & Zhou 23742* (PE); Somang, 42 km milestone of Shuanjingsi–Barkam highway, *Zhang & Zhou 22675* (PE). Luhuo: *P. C. Tsoong 5024* (PE); Zhehor, by river, *J. S. Ying 4582* (PE). Mabian: *E. T. Wang 22930* (PE). Maowen: Mt. Mafang, *Sichuan Econom. (A-59) 2554* (PE); Xiang-Naha, Sanlonggou, *He & Zhou 13338* (PE). Mianning: Yejin Township, *S. F. Zhu 20491*(PE); Huning distr., Jiexingou, *S. Jiang 5768* (PE). Muli: Wa-chin, *T. T. Yu 6137* (PE). Qianning: S of town, *Jiang & Jin 2113* (PE); to Dawu, *Zhang & Lang 57* (PE). Sêrtar: 1 km S of Wungda, *S. Jiang 9082* (PE). Songpan: Housigou, *S. Jiang A-7275* (PE); Mont. Occid. *H. Smith 2499* (PE). Tianquan: Mt. Erlong, Xiaoniujingou, around Xiashan, *Hu & He 10088* (PE). Wenchuan: Wolong Township, *Sichuan-Econom. A59-2290* (PE); Wolong Nature Reserve, Mt. Balang, *Hong & Zhu PB85019* (PE). Xiaojin: Xihekou, Niuchanggou, *Zhang & Ren 6322* (PE); Luobigou, Yangpingkou, *Zhang & Ren 6082* (PE). Yajiang: Mt. Ermin, *Sichuan Plants Collection 0905* (PE); Tanjiao to Malangcuo, *J. S. Ying 3113* (PE). Zamtang: Lukesi Temple, right bank, *S. Jiang 8930* (PE); 10 km W of Gangmuda, *S. Jiang 8965* (PE). **Xizang** (Tibet): Jomda: Gamtog distr., *Qinghai-Xizang Exped. Vegetation Group 9893* (PE).

2. Paeonia intermedia C. A. Meyer, in Ledebour, Fl. Altaic 2: 277. 1830. *Paeonia anomala* var. *hybrida* f. *intermedia* (C. A. Meyer) Trautvetter, Enum. Pl. Songor. 88. 1860. *Paeonia hybrida* var. *intermedia* (C. A. Meyer) Krylov, Fl. Altaya 1: 47. 1901. *Paeonia anomala* subsp. *intermedia* (C. A. Meyer) Trautvetter, in B. Fedtschenko, Trudy Imp. S. Petersburg. Bot. Sada 23: 351. 1904. *Paeonia anomala* var. *intermedia* (C. A. Meyer) O. & B. Fedtsch., Beih. Bot. Centralbl. 18: 216. 1905. TYPE: the Altai Mountains, *Ledebour s.n.* (lectotype, designated here, K!).

Paeonia majko N. Ketzchoweli, Notul. Syst. Geogr. Inst. Bot. Tiphlis. fasc. 21: 17. 1959. TYPE: Georgia. Kartly, between Igoeti and Lamitskali, 16 May 1958. *N. Ketschoweli s.n.* (holotype, TBI!).

Paeonia intermedia subsp. *pamiroalaica* P. N. Ovchinnikov, in Fl. Tadzhikistanskoi SSR. 4: 6–10 & 531. 1975. TYPE: Tadzhikistan: declivitas australis jugi Hissarcic, ad ripam dextram fl. Maichura, 5 km ab ostio, 2500 m, 12.06.1971, *A. A. Gleboca 6* (holotype, TAD not seen).

The species has long been identified as *Paeonia anomala* (Pan, 1979), treated as a variety of *P. hybrida* (Krylov, 1901; Schipczinsky, 1921, 1937; Gamaulova, 1961), a variety of *P. anomala* (Fedtschenko, 1905; Stern, 1946; Pan, 1979), a subspecies of *P. anomala* (Trautvetter, 1904), or even as a form of *P. anomala* var. *hybrida* (Trautvetter, 1860). These diverse and erroneous assignments were made because: (1) the identity of *P. anomala*, *P. intermedia*, and *P. hybrida* was not previously clear; (2) previous authors emphasized the taxonomic value of indumentum on carpels; and (3) the characters of roots and calyces and their correlation were not considered. Examination of the types of the three taxa and extensive observations on herbarium specimens and natural populations (Table 1) show that *P. intermedia* C. A. Meyer is an independent species, distinctly differing from *P. anomala* by its lateral roots tuberous to long-fusiform, sepals mostly (at least 2) rounded at apex but not caudate. Also different from *P. anomala*, *P. intermedia* prefers relatively sunny and dry habitats. Carpels vary from 1 to 5 in number, and from glabrous to densely tomentose. Ovchinnikov (1975) properly treated the peony in Tadzhikistan as *P. intermedia*, but his description of the new subspecies *pamiroalaica* is unjustifiable. His description and our extensive observations have not revealed any significant difference.

This species is widely distributed in northern Xinjiang, China (south to the Tienshan), Kazakhstan, Kirghizia, Tadzhikistan, Uzbekistan, and the Altai of Russia. One small isolated population was found in Georgia (Hong & Zhou, 2003) (Fig. 3). It grows in grassy and shrubby slopes, meadows, steppes, or in sparse woods, at altitudes from 900 to 3250 m.

Phenology. This species flowers from late May to late June and fruits from August to September.

Chromosomes. $2n = 10$ (Hong et al., unpublished).

Additional specimens examined. CHINA. **Xinjiang:** Altai Mt.: *Acad. Sinica Xinjiang Integr. Exped. 10657*

(PE). Altay: Qiao'ati, *G. L. Zhu et al. 6325* (PE); to Halamaryi, *Acad. Sinica Xijiang Exped. 10227* (PE); Klasu Gou, *R. C. Ching 2433* (PE); Haxiong Gou, *T. Y. Chou 652100* (XJBI); Mt. Halamaryi, *D. Y. Hong et al. Population No. 2* (PE); Xiaodong Gou, *D. Y. Hong et al. Population No. 4* (PE). Barkol: Nanshan, *s. coll. 780* (XJBI). Fuhai: Fuhai Forest Farm, *G. L. Zhu 5665* (PE); N slopes, *T. Y. Chou et al. 652150* (PE, XJBI). Fukang: Tienci, Shimen, *D. Y. Hong et al. 0190* (PE). Fuyun: Mica No. 3 Mine, *Integr. Exped. s.n.* (XJBI); Mica No. 4 Mine, *Integr. Exped. s.n.* (XJBI). Habahe: Tielieke, *Kelimu 10171* (XJBI); Wuzliti, *Kelimu 10614* (XJBI). Hoboksar: *Songshu Gou s. coll. 7385* (XJBI); Mt. Qiaganebo, *Integr. Exped. 10563* (PE, XJBI). Huocheng: Aksu Commune, *Y. R. Ling 74848* (PE); Daxigou, *Acad. Sinica Exped. 10402* (PE); Xin'ertai, Yeguolin, *C. W. Chang et al. 3316* (XJBI); Xiaoxigou, *A. R. Li & J. N. Zhu 10414* (PE, XJBI). Mori: Nangou, *S. L. Chen 0040* (PE). Qapqal: 58 km from Yining to Zhaosu, *Inst. Biology and Pedology 66* (XJBI). Qitai: Biliuhe, *J. C. Zhao 82-4288* (PE, XJU); Kuangou, *Biology 81-8381574* (XJBI); Tangfangmen Forest Farm, *Integr. Inst. Bio. Res. 5788* (XJBI); Yuejin Commune, *S. Q. Lin et al. 34* (XJBI). Tacheng: Mt. Baerleike, N slope, *Integ. Exped. 1200* (XJBI). Toli: Mt. Albakzin, mountain slope, *K. C. Kuan 2611* (PE, XJBI). Xinyuan: Nanshan, *T. Y. Chou et al. 650392* (PE). Yining: Yining Forest Farm, Jirtoulong valley, *D. Y. Hong et al. Population 1 & 092* (PE). Yumin: The Wild Bada *Prunus* Nature Reserve, *J. C. Zhao 85-293* (PE, XJU). GEORGIA. **Kartly:** between Lamistskali and Igoeti, *Hong & Zhou H99033* (PE). KAZAKHSTAN. **Ili-Pribalkhash:** NW ridges of Mt. Kirgizsky Range, upper Sugata River, *V. Golos-Kokov s.n.* (LE); Issyk-Kul Province, Santash, Dongulsky garden, *Aidarova & Kashenko s.n.* (LE); Semirechensk Province, N slope of Alatau, between Verny to Kastek mountain pass, *V. Ladygin s.n.* (LE); SW Songorian Alatau, Mt. Emelsky Range, Mt. Matai, *V. Goloskokov s.n.* (LE); Taldy-Kurgan Province, Mt. Altyn-Emel Range, Mt. Engi-Altyn-Emel pass to road Sary-Ozek-Dzharkent, *Grubov & Luboarsky 229* (LE); Zailiisky Alatau, Usun-Kargali River Valley, W Sukonnaya Fabrika, *Y. Goloskokov* (LE). **E. Kazakhstan:** Mt. Kalbinsky Range, Mt. Kok-tau, near Sabinskie Lake, *A. Yunatov 24* (LE); Semipalatinsk Province, Zaisan distr., Kusto Gorge, *B. Shishkin s.n.* (LE); Zaisan distr., near Kenderlyk, *B. Shishkin s.n.* (LE); near Zaisan, Mt. Kichken-tau, *Tatarowa & Borsowa 52* (LE). **Mountain Kazakhstan:** Semirechensk Prov., Songorian Alatau, S of Lepsinsk, *R. Rozhevits 55* (LE); W ridges of Songorian Alatau, Koksu Gorge, near Koksuisky, *V. Goloskokov* (LE); Tarbagatai, Chenarak, steppes, *Grigoriev & Buhaeva 298* (LE); Mt. Tsarytsynsky Pass, deep gorge from the pass, *Schipczinsky 125* (LE). **S. Kazakhstan:** Mt. Chatkalsky Range, Chatkal Valley, Mt. Piazak, *O. Knorring 60* (LE); Prichuisky Mujun(Kum), Sulunger Gorge, *F. Zapriagaev 66* (LE). KIRGHIZIA. **Dzhalalabad Province:** Bazar-Kurgan distr., Mt. Fergansky Range, S slopes, near AK-Terek, *Lebedeva & Faleeva s.n.* (LE); Kara-Alma, Toguz (Bulak), N slopes, *Poniatovskaya, s.n.* (LE); Tianshan, Mt. Ketmen Range, Mt. Elchin-Ustriuk, Kizilbulak Gorge, *s. coll. s.n.* (LE). **Fergana Province:** Kirgizsky Alatau, Makbal Gorge, Ty-Karyn River, *G. Igolkin 97* (LE); Oshsky distr., Ak-Bura valley, Mt. Kanida Pass, *O. Knorring 25* (LE). **Semirechensk Province:** Pishpeksky distr., Uzungyrskaya Volost, Mt. Aleksandrovsky Range, Mt. Shekule N slope, *A. Savenkova 29* (LE). RUSSIA. **Altai:** *Alex Shrenk s.n.* (LE); Altai, Barnaul Province, between Kalmytskie Mysy & Mahanova, *P. Krylov s.n.* (LE). TADZHIKISTAN. **Gissarsky Mountain Range:** Buhara, Gissar, Mtn. Zarkamar Pass, *V. Lipsky 1697* (LE). Darvazsky Mtn. Range, N slopes, left bank of Zarako River, opposite Havdak, *Shinova & Kinzikaeva 1550* (LE). Imam-Askari, Mt. W of Darai-Imam, *Bochantsev & Egorova 1014* (LE). Peter I Range, N slopes, Nazarak Valley, upper reaches, 15 km S of Tadzhikabad, *Ladygina, Ikonnikov & Fridman 1337* (LE). Vahshsky Mtn. Range, Mt. Hozreshi-Sho, above Sary-Hosor, *Sidorenko 185* (LE). Varzob Valley, right bank of Maihur Gorge, NE slope, *Stepanenko & Kudriashova 2514* (LE); Mountain pass between rivers Havag & Ketsgug, *N. Gontscharow 2051* (LE); upper Horanchon, *Zapriagaev 351* (LE). UZBEKISTAN. **Tashkent Province:** Bolshoy Chimgan, *Z. von Minkwitz 1190* (LE); Bolshoy Chimgan, N stony slopes, *V. Bochantsev 547* (LE).

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Appendix 1

Index to exsiccatae examined

The figures in parentheses represent: 1a = *Paeonia anomala* subsp. *anomala*; 1b = *P. anomala* subsp. *veitchii*; 2 = *P. intermedia*.

Acad. Sinica Bot. Inst. Exped. Xinjiang 1803 (PE, XJBI) (2); Acad. Sinica Exped. 10402 (PE) (2); Acad. Sinica Xinjiang Exped. 2496 (PE, XJBI) (1a), 10227 (PE) (2); Acad. Sinica Xinjiang Integr. Exped. 10657 (PE) (2); Agr. College 1051 (PE) (2); Aidarova & Kashenko s.n. (LE) (2); Alexandrov, P. 179 (LE) (1a), 219 (LE) (1a); Alex Shrenk s.n. (LE) (2).

Bai, J. L. 8613 (NWTC) (1b); Beresowskii, M. s.n. (LE) (1b, type of *Paeonia beresowskii* Komarov); Biology Exped. 79250198 (XJBI) (2), 81-8330478 (XJBI) (2); Bochantsev, V. 547 (LE) (2); Bochantsev & Egorova 1014 (LE) (2); Borovikov, G. s.n. (LE) (1a); Borovikov et al. s.n. (LE) (1a).

Chang, C. W. 11356 (XJBI) (1a); Chang, C. W. et al. 3316 (XJBI) (2), 4037 (XJBI) (2), 4357 (XJBI) (1a), 10255 (XJBI) (1a); Chen & Ju s.n. (NWTC) (1b); Chen, S. L. 0040 (PE) (2); Cherepnin s.n. (LE) (1a); Ching, R. C. 1803 (PE) (1a), 2433 (PE) (2), 2496 (PE) (1a); Chou, T. Y. 652100 (XJBI) (2); Chou, T. Y. et al. 650392 (PE) (2), 650868 (PE, XJBI) (2), 652150 (PE, XJBI) (2); Cui, N. R. 091 (XJNU) (1a), 86624 (XJNU) (1a); Cui, Y. W. 4348 (PE) (1b), 10281 (PE) (1b).

Dolenko, G. 108 (LE) (1a); Dranitsyn & Kochubei s.n. (LE) (1a).

Ermolajeva, M. s.n. (LE) (1a); Evseeva, Z. 4406 (LE) (1a).

Fang, W. P. 4213 (LE) (1a), 6037 (LE) (1a); Farrer, R. 67 (E) (1b, type of *Paeonia woodwardii* Stapf ex Cox); Fedorov & Iljina 72 (LE) (2), 128 (LE) (2); Fu, K. J. 4441 (PE) (1b); Fu, T. K. 834 (PE) (1b).

Ganeshin, S. s.n. (LE) (1a); Gansu Herbs Group s.n. (NWTC) (1b); Genina, S. s.n. (LE) (1a); Gansu-Qinghai Exped. 2493 (PE) (1b); Goloskokov, V. s.n. (LE) (2); Gontscharow, N. 2051 (LE) (2); Gorodkov, B. 512 (LE) (1a); Grigoriev & Buhaeva 298 (LE) (2); Grubov & Luboarsky 229 (LE) (2); Guo, B. Z. 6767 (HNWP) (1b), 7010 (HNWP) (1b), 7396 (HNWP) (1b), 10186 (HNWP) (1b), 10232 (HNWP) (1b); Guo & He 9012 (HNWP) (1b); Guo & Wang 6008 (HNWP) (1b), 6717 (HNWP) (1b), 25058 (HNWP) (1b); Guo & Yang 9608 (HNWP) (1b).

Hanminchun, V. 515 (LE) (1a); Hao, K. S. 779 (PE) (1b); He, Y. Q. 4516 (PE) (1b), 4915 (PE) (1b); He, Z. 12339 (PE) (1b); He & Zhou 13338 (PE) (1b); Hong D. Y. et al. Population 2 (PE) (2), Population 3 (PE) (1a), Population 4 (PE) (2), Population 5 (PE) (1a), Population 1 (PE) (2), Population 0190 (PE) (2); Hong D. Y. & Zhong PB82105 (PE) (1b); Hong D. Y. & Zhu PB85019 (PE) (1b), PB85040 (PE) (1b), PB85065 (PE) (1b); Hong, Luo & He H95034 (A, CAS, K, MO, PE, US) (1b); Hong & Zhou H99033 (PE) (2); Hsia, W. Y. 4539 (PE) (1b), 4571(PE) (1b), 5707 (PE) (1b); Hu, W. G. 13050 (PE) (1b); Huanghe Exped. 1689 (PE) (1b), 3183 (PE) (1b), 4655 (PE) (1b), 1735 (PE) (1b); Hu & He 10088 (PE) (1b), 10373 (PE) (1b), 10463 (PE) (1b), 11173 (PE) (1b); Huang, Luo & Jiang 730 (PE) (1b).

Igolkin, G. 97 (LE) (2); Ikonnikov & Fridman 892 (LE) (2); Iljin, V. s.n. (LE) (1a); Integr. Exped. 630 (XJBI) (1a), 1200 (XJBI) (2), 7305 (XJBI) (1a), 10563 (PE, XJBI) (2), 11829 (XJBI) (1a), s.n. (XJBI) (2); Integr. Inst. Hydrol. Pedol & Biol. Res. 5788 (XJBI) (2).

Jia, S. X. 229 (PE) (1b); Jiang & Jin 00386 (PE) (1b), 2113 (PE) (1b); Jiang & Xiong 34242 (PE) (1b), 34319 (PE) (1b), 35625 (PE) (1b); Jiang, S. 5768 (PE) (1b), 8874 (PE) (1b), 8930 (PE) (1b), 8965 (PE) (1b), 9082 (PE) (1b), A-7162 (PE) (1b), A-7275 (PE) (1b); Jiang, X. C. 36014 (PE) (1b), 36433 (PE) (1b).

Kelimu 10171 (XJBI) (2), 10369 (XJBI) (2), 10614 (XJBI) (2); Keller, B. s.n. (LE) (1a); Ketzchoweli, N. s.n. (TBI) (2, type of *Paeonia majko* N. Ketzchoweli); Kildushewsky, I. 150/22 (LE) (1a); Klements, E. 4d (LE) (1a), 11a (LE) (1a); Klopotov, B. 113 (LE) (1a), 180 (LE) (1a); Knorring, O. 25 (LE) (2), 66 (LE) (2); Kokulin, S. 254 (LE) (1a); Kolomoitseva, S. 236 (LE) (1a); Komarov, V. s.n. (LE) (1a); Korovkin, A. 290 (LE) (1a); Krasnoborov, I. 6765 (LE) (1a); Krishtofowich, A. s.n. (LE) (1a); Krylov, P. s.n. (LE) (2); Kuan, K. C. 2611 (PE, XJBI) (2), 77309 (PE) (1b); Kuan et al. 243 (PE) (1b), 352 (PE) (1b); Kucherovskaya, S. 282 (LE) (1a); Kuminova & Alexeeva s.n. (LE) (1a); Kuvajev & Sabitov s.n. (LE) (1a); Kuznetsov, I. 53 (LE) (1a), 114 (LE) (1a), 193 (LE) (1a), 4661 (LE) (1a); Kuznetsov, N. 199 (LE) (1a), 1991 (LE) (1a).

Ladygin 92 (LE) (1a), s.n. (LE) (2); Ladygina et al. 1337 (LE) (2); Lashinsky & Ronginskaya 973 (LE) (1a); Lebedeva & Faleeva s.n. (LE) (2); Ledebour, s.n. (K) (2, type of *Paeonia intermedia* C. A. Meyer); Li, A. R. & Zhu, J. N. 10414 (PE, XJBI) (2); Li, P. X. 10100 (PE) (1b), 10137 (PE) (1b), 10143 (PE) (1b); Li, X. 70247 (PE) (1b), 70441 (PE) (1b), 70510 (PE) (1b), 70685 (PE) (1b), 70719 (PE) (1b), 70867 (PE) (1b), 70903 (PE) (1b), 71029 (PE) (1b), 71087 (PE) (1b), 71196 (PE) (1b), 71645 (PE) (1b), 74842 (PE) (1b), 74936 (PE) (1b), 77248 (PE) (1b, type of *Paeonia veitchii* var. *leiocarpa* W. T. Wang & S. H. Wang); Li, X. Y. 870147 (SHI) (1a), 870169 (SHI) (2); Lian & Chen 31 (NWTC) (1b), 72 (NWTC) (1b); Lian et al. 378 (HNWP) (1b), 79179 (NWTC) (1b); Licent, P. 2022 (PE) (1b); Lin, S. Q. et al. 34 (XJBI) (2); Ling, Y. R. 1141 (PE) (1a, type of *Paeonia sinjiangensis* K. Y. Pan), 74243 (PE) (2), 74848 (PE) (2), 74849 (PE) (2); Liou, K. M. 5659 (PE) (1b), 5970 (PE) (1b), 6019 (PE) (1b), 6178 (PE) (1b); Lipsky, V. 1697 (LE) (2); Liu & Luo 1040 (HNWP) (1b); Liu & Shen 8308 (XJBI) (1a); Liu, S. W. 2115 (HNWP) (1b); Lomonosova & Ivanova 89 (LE) (1a); Long, X. F. 85 (NWTC) (1b).

Maltsev, N. 79 (LE) (1a); Mao, Z. M. 10413 (XJBI) (1a); Mihno, P. s.n. (LE) (1a); Minkwitz Z. von 1190 (LE) (2); Morgan, P. 23 (K) (1a).

Nanshui-Beidiao Exped. 02912 (PE) (1b).

Pharmac. Exped. 2019 (PE) (1b); Pobedimova 697 (LE) (1a); Pohle & Rozhdestvensky s.n. (LE) (1a); Polozhii & Kandasova s.n. (LE) (1a); Poniatovskaya s.n. (LE) (2); Price, M. P. 293 (LE) (1a).

Qing, Z. Y. 1218 (HNWP, PE) (1b); Qinghai-Xizang Exped. Veget. Group 034 (PE) (1b, type of *Paeonia veitchii* var. *uniflora* K. Y. Pan), 9893 (PE) (1b); Qu, Z. X. 2792 (PE) (1b).

Reznichenko, V. 49 (LE) (1a), 58 (LE) (1a); Reznichenko, V. & A. 106 (LE) (1a), 360 (LE) (1a), s.n. (LE) (1a); Rock, J. F. 12260 (PE) (1b), 12829 (PE) (1b), 13127 (PE) (1b); Rohderi, I. s.n. (LE) (1a); Rozhevits, R. 55 (LE) (2); Rubin, A. s.n. (LE) (1a); Rubin & Maskil, s.n. (LE) (1a).

Sanadze et al. s.n. (TBI) (2); Savenkova, A. 29 (LE) (2); Schipczinsky 125 (LE) (2); s. coll. Siberia, (LINN) (1a, type of *Paeonia anomala* Linnaeus); Sedelnikov, A. s.n.

(LE) (1a); S. Gansu Grassland Exped. 681 (NWTC) (1b); Shanxi Exped. 684 (PE) (1b); Shanxi Exped. Wang & Tian 594 (PE) (1b); Shinova & Kinzikaeva 1550 (LE) (2); Shishkin, B. s.n. (LE) (2); Shliahtin, A. s.n. (LE) (1a); Shukin, S. s.n. (LE) (1a); Sichuan-Econom. A59-0246 (PE) (1b), A59-1001 (PE) (1b), A59-1208 (PE) (1b), A59-2554 (PE) (1b), Sichuan-Econom. & Ya 838 (PE) (1b); Sichuan Plants Collection 0905 (PE) (1b); Sidorenko 185 (LE) (2); Smirnov, V. s.n. (LE) (1a); Smith, H. 2499 (PE) (1b); Sochava, V. 100 (PE) (1b); Sokolov, P. 13a (LE) (1a); Song, Z. P. 38544 (PE) (1b), 39107 (PE) (1b); Stepanenko & Kudriashova 2514 (LE) (2); Suhareva, A. s.n. (LE) (1a).

Tang, T. 938 (PE) (1b); Taohe Exped. 3243 (PE) (1b); Tatarova & Borsowa 52 (LE) (2); Tolmatschew, I. 247 (LE) (1a); Tomin, M. 67 (LE) (1a); Tripolitova, T. s.n. (LE) (2); Troitsky, W. s.n. (LE) (1a); Tsoong, P. C. 5004 (PE) (1b), 5024 (PE) (1b), 8842 (PE) (1b); Tu, T. H. 362 (PE) (1b), 4329 (PE) (1b); Tugarinov, A. s.n. (LE) (1a); Turczaninow, s.n. (LE) (1a).

Varentsov, V. s.n. (LE) (1a); Vereshagin, V. 296 (LE) (1a), 345 (LE) (1a); Verhovskaya & Mishin 104 (LE) (1a); Vislouh, E. 73 (LE) (1a); Vydrin, A. s.n. (LE) (1a).

Wang, F. T. 22930 (PE) (1b); Wang, J. Q. 197 (NWTC) (1b); Wang, Q. R. 1869 (NWTC) (1b), 7034 (NWTC) (1b), 7270 (NWTC) (1b); Wang, S. X. 1065 (HNWP) (1a); Wang, T. P. 197 (NWTC) (1a), 15240 (NWTC) (1a), 4594 (NWTC) (1a), 6944 (PE) (1b); Wang, W. Y. 26771 (HNWP) (1b), 26818 (HNWP) (1b), 27060 (HNWP) (1b); Wang, W. Y. et al. 27347 (HNWP) (1b); Wang & Zhou 19 (HNWP) (1b), 198 A (HNWP) (1b).

Xinjiang Branch Acad. Sinica 012 (XJBI (1a); Xu, L. R. s.n. (PE) (1a).

Yakovlev, D. 69 (LE) (1a); Yan, M. S. 1843 (NWTC) (1b); Ying, J. S. 3113 (PE) (1b), 3869 (PE) (1b), 4582 (PE) (1b), 4591 (PE) (1b); Ying, T. H. 995 (PE, SHMU) (1a), 1001 (PE, SHMU) (1a), 1006 (PE, SHMU) (1a), 1007 (SHMU, PE) (1a, type of *Paeonia altaica* K. M. Dai & T. H. Ying), 1008 (PE) (1a), 1009 (PE, SHMU) (1a), 1010 (PE, SHMU) (1a), 1011 (PE, SHMU) (1a), 1014 (PE, SHMU) (1a), 1022 (PE, SHMU) (1a); Yu et al. 68 (PE) (1b); Yu, T. T. 2200 (PE) (1b), 6137 (PE) (1b); Yunatov, A. 24 (LE) (2); Yurchenko, P. s.n. (LE) (1a).

Zapriagaev, F. 66 (LE) (2), 351 (LE) (2); Zhang, F. M. 90-346 (XFNU) (1a); Zhang, G. Z. 005 (HNWP) (1b); Zhang & Lang 57 (PE) (1b); Zhang & Li 0502 (HNWP) (1b); Zhang & Ren 5572 (PE) (1b), 6082 (PE) (1b), 6322 (PE) (1b); Zhang, Z. H. et al. 0097 (HNWP) (1b), 0414 (HNWP) (1b), 4291 (HNWP) (1b), 4317 (HNWP) (1b), 4320 (HNWP) (1b); Zhang & Zhou 22092 (PE) (1b), 22155 (PE) (1b), 22675 (PE) (1b), 23742 (PE) (1b); Zhao, J. C. 82-293 (PE, XJU) (2), 82-4288 (PE, XJU) (2), s.n. (PE, XJU) (2); Zhen, S. X. 0351 (PE) (1b); Zhou, H. J. 708 (NWTC) (1a); Zhou, L. H. 2528 (HNWP) (1b); Zhu, G. L. 5665 (PE) (2), 5755 (PE) (1a), 6345 (PE) (1a), 80006 (NWTC) (1b); Zhu, G. L. et al. 6325 (PE) (2), 6386 (PE) (2); Zhu, S. F. 20491 (PE) (1b).

PHYLOGENY OF *SMELOWSKIA* AND RELATED GENERA (BRASSICACEAE) BASED ON NUCLEAR ITS DNA AND CHLOROPLAST *trn*L INTRON DNA SEQUENCES[1]

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Abstract

Using sequence data from the ITS region (internal transcribed spacers ITS1 and ITS2 of nuclear ribosomal DNA and the 5.8S rRNA gene) and chloroplast DNA sequence data from the *trn*L intron, we examined the evolutionary relationships of Old and New World *Smelowskia* species with its putatively related genera (Brassicaceae). ITS and *trn*L sequence data were obtained from all 13 *Smelowskia* species and from 13 taxa of the related genera *Descurainia*, *Ermania*, *Gorodkovia*, *Hedinia*, *Polyctenium*, *Redowskia*, *Sinosophiopsis*, and *Sophiopsis*. Results from maximum parsimony analyses showed a polyphyletic origin for *Smelowskia*, with the taxa split into two major clades. *Smelowskia* taxa plus *Ermania*, *Gorodkovia*, *Hedinia*, *Redowskia*, *Sinosophiopsis*, and *Sophiopsis* formed one clade (*Smelowskia* s.l. clade), whereas the other clade included *Smelowskia holmgrenii* (Holmgrenii subclade) and the genus *Polyctenium* (*Polyctenium* subclade). *Descurainia* formed a separate clade. ITS and *trn*L molecular data, along with a comparison of key morphological traits for each genus, support recognition of a single genus that would include *Smelowskia*, the three monotypic genera *Ermania*, *Gorodkovia*, and *Redowskia*, as well as the genera *Hedinia*, *Sinosphiopsis*, and *Sophiopsis* (although not all species were examined in these genera). The molecular data are consistent with an Asian origin for *Smelowskia* s. str., followed by diversification in Asia and North America, subsequent to migration into arctic-alpine regions of western North America. ITS sequence divergence estimates ranged from 0 to 4.1% within *Smelowskia* s. str., and up to 6.45% within the *Smelowskia* s.l. clade; whereas *trn*L sequence divergence estimates ranged from 0 to 1.85% within *Smelowskia* s. str., and up to 3.71% within the *Smelowskia* s.l. clade, indicating pleistocenic speciation within *Smelowskia* as a whole.

Key words: Brassicaceae, *Descurainia*, *Ermania*, *Gorodkovia*, *Hedinia*, ITS, *Polyctenium*, *Redowskia*, *Sinosophiopsis*, *Smelowskia*, *Sophiopsis*, *trn*L.

The Brassicaceae are a large family of about 340 genera and over 3350 species distributed throughout the world, primarily in temperate regions (Al-Shehbaz, 1984; Appel & Al-Shehbaz, 2002). It is a well-defined family easily distinguished from the related Cleomaceae by floral and fruit morphology (i.e., cruciform corolla, tetradynamous stamens, and septate capsular fruits (Hall et al., 2002)). Tribal classification of the family is, however, controversial, and its phylogeny requires clarification (Koch, 2003; Koch et al., 2003). The characters traditionally used at the tribal rank are few and include orientation of the radicle in the embryo, number of rows of seed in each locule, calyx orientation, trichome type, fruit compression type (length-width ratio), and features of the nectaries. Several tribal systems have been proposed, and most of the traditional groupings, with the exception of the Brassiceae and perhaps the Heliophileae, are not monophyletic (Koch et al., 2001, 2003; Appel & Al-Shehbaz, 2002). Generic delimitation is also a frequently encountered problem (Al-Shehbaz, 1984; Appel & Al-Shehbaz, 2002), and as many other genera of the family, *Smelowskia* C. A. Mey. is artificially delimited and lacks unique synapomorphies (Table 1). All species are perennials with

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Table 1. Morphological comparison of *Smelowskia* and related genera (Descurainiinae).

	Descurainia	*Ermania*	*Gorodkovia*	*Hedinia*	*Polyctenium*	*S. holmgrenii*	*Redowskia*	*Sinosophiopsis*	*Smelowskia*	*Sophiopsis*
Duration	annual or perennial	perennial	perennial	annual or perennial	perennial	perennial	perennial	annual	perennial	annual or perennial
Thichomes	dendritic	dendritic, few simple or forked	mostly simple, fewer forked	dendritic, 1–3-forked, few simple	forked and simple, few subdendritic	simple, few forked	dendritic, few forked	simple and forked	dendritic, forked, rarely few simple	dendritic, forked, or few simple
Glandular papillae	present	absent	absent	absent	absent	absent	absent	absent	absent	absent
Lower leaves	(1–)2–3-pinnatisect	flabellate or toothed	1-pinnatisect	1–2-pinnatisect	1-pinnatisect	entire	2-pinnatisect	1-pinnatisect	1–2-pinnatisect, flabellate, or entire	1–2-pinnatisect
Leaf texture	herbaceous	herbaceous	herbaceous	herbaceous	rigid, leathery	rigid, leathery	herbaceous	herbaceous	herbaceous	herbaceous
Raceme	ebracteate, rarely bracteate	ebracteate	ebracteate	bracteate	ebracteate	ebracteate	ebracteate	bracteate or ebracteate	ebracteate	bracteate or ebracteate
Petal color	yellow, rarely white	white or purple	white	white	white, rarely purple	white	white	white	white, purple, or creamy white	yellow
Median nectaries	present	present	present	absent	present	present	present	present	present	present
Ovules per ovary	5–100	10–18	6–16	18–46	12–40	5–12	6–10	20–40	6–30	4–12
Fruit type	silique, rarely silicle	silique	silique	silicle, rarely siliques	silique or silicle	silique	silicle	silique	silique or silicle	silique or silicle
Fruit shape	linear or oblong, rarely clavate or elliptic	linear to oblanceolate	linear to oblanceolate	orbicular, oblong, or elliptic	linear, oblong, or ovate	linear	suborbicular or broadly fusiform	linear	linear, oblong, obovoid, ellipsoid, or lanceolate	linear, oblong, obovoid, or ellipsoid
Fruit cross section	terete	latiseptate	latiseptate	angustiseptate	terete or slightly angustiseptate	terete	angustiseptate	terete	terete, latiseptate, or angustiseptate	terete
Valve midvein	prominent or obscure	prominent	prominent	prominent	obscure	obscure	prominent	obscure	prominent	prominent
Valve keel	absent	absent	absent	present	absent	absent	present	absent	present or absent	absent
Style	obsolete, rarely short	short	short	short	prominent	prominent	prominent	short	obsolete, short, or prominent	obsolete or short

Table 1. Continued.

	Descurainia	*Ermania*	*Gorodkovia*	*Hedinia*	*Polycterium*	*S. holmgrenii*	*Redowskia*	*Sinosophiopsis*	*Smelowskia*	*Sophiopsis*
Stigma	entire	entire	entire	entire	entire	entire	slightly 2-lobed	entire	entire	entire
Septum	complete, rarely perforate	complete	complete	complete, rarely perforate	complete	complete	perforate	complete	complete or perforate	complete or perforate
Seed arrangement	uniseriate, rarely biseriate	uniseriate	biseriate	uniseriate	uniseriate	uniseriate	biseriate	uniseriate	uniseriate	uniseriate
Cotyledons	incumbent	accumbent	accumbent	incumbent	incumbent	incumbent	incumbent	incumbent	incumbent	incumbent
Number of species	40	1	1	4	2	1	1	3	7–14	4
Geographical distribution	Eurasia, North & South America, N Africa	northeast Asia (Russia, Siberia)	northeast Asia (Russia, Siberia)	central Asia (Himalayas, Mongolia, Russia, China)	western U.S.A. (CA, ID, NV, OR)	western U.S.A. (NV)	Russia (Siberia)	China	western Asia and western North America	central Asia

1- or 2-pinnatisect (rarely entire) leaves, ebracteate racemes, white, purple, or creamy white flowers, distinct median nectaries, 6 to 30 ovules per ovary, variously shaped (linear, oblong, obovoid, ellipsoid, or lanceolate) fruits, a prominent midvein on the valves, entire stigmas, uniseriately arranged seeds, and incumbent cotyledons. The majority of species have soft, dendritic and forked hairs, herbaceous, divided leaves soft in texture, and flattened or angled fruits, but *S. holmgrenii* does not have this combination of characters.

Smelowskia has been variously delimited (taxonomic treatments vary from 7 to 14 species), with several segregate genera placed in subtribe Descurainiinae of the tribe Sisymbrieae (Drury & Rollins, 1952; Botschantzev, 1968; Velichkin, 1979; Rollins, 1993; Czerepanov, 1995; Mulligan, 2001; Zhou et al., 2001). As currently circumscribed, *Smelowskia* includes 13 species, of which 7 (*S. americana, S. borealis, S. holmgrenii, S. johnsonii, S. media, S. ovalis, S. pyriformis*) are North American, 5 (*S. alba, S. bifurcata, S. calycina, S. inopinata, S. pectinata*) are central and north Asian, and 1 (*S. porsildii*) occurs on both continents. Names of accepted taxa, synonyms, and excluded names in *Smelowskia* are listed in Table 2. Varieties of *S. calycina* previously recognized in North America are treated as distinct species.

Schulz (1924, 1936) placed *Smelowskia* in the tribe Sisymbrieae subtribe Descurainiinae, along with *Descurainia* Webb & Berth., *Hugueninia* Rchb., *Redowskia* Cham. & Schltdl., *Robeschia* Hochst. ex O. E. Schulz, *Sophiopsis* O. E. Schulz, and *Trichotolinum* O. E. Schulz. He divided *Smelowskia* into section *Smelowskia* (*S. alba, S. calycina, S. lineariloba*, and *S. ovalis*) and section *Polyctenium* (Greene) O. E. Schulz (*S. fremontii*). In North America, Rollins (1938) recognized *Smelowskia* (*S. calycina* and *S. ovalis*) and *Polyctenium* Greene (*P. fremontii*) as closely related genera.

Hultén (1945) placed the monotypic genera *Melanidion* Greene (*M. boreale* Greene) (Greene, 1912) and *Acroschizocarpus* Gombócz (*A. kolianus* Gombócz) (Gombócz, 1940) in *Ermania borealis* (Greene) Hultén. However, this transfer was invalid, as the generic name *Ermania* (Chamisso, 1831) was not validated until 1956 by Botschantzev (reviewed in Al-Shehbaz, 2001). Drury and Rollins (1952) supported the congeneric status of *Melanidion* and *Acroschizocarpus* and placed them in *Smelowskia* rather than *Ermania* Cham. ex Botsch., as *S. borealis* var. *borealis* and var. *koliana*, respectively. Rechinger (1954) reduced his (Rechinger, 1951) monotypic *Chrysanthemopsis* (*C. koelzii*

Table 2. Species of *Smelowskia* as recognized by various authors. Species in boldface (13) are accepted in this account as members of *Smelowskia*.

Species	Drury & Rollins (1952) Rollins (1993)	Botschantzev (1968)	Velichkin (1979)	Czerepanov (1995)	This account
S. alba (Pall.) Regel		*S. alba*	*S. alba*	*S. alba*	*Smelowskia alba*
S. alpina C. A. Mey.					*Hornungia alpina*
S. altaica (Pobed.) Botsch.				*Hedinia altaica*	*Hedinia altaica*
S. americana (Regel & Herder) Rydb.	*S. calycina* var. *americana*		*S. americana*		*Smelowskia americana*
S. annua Rupr.					*Sophiopsis annua*
S. asplenifolia Turcz.				*S. bifurcata*	*Smelowskia bifurcata*
S. bifurcata (Ledeb.) Botsch.		*S. bifurcata*	*S. bifurcata*	*S. bifurcata*	*Smelowskia bifurcata*
S. borealis (Greene) W. H. Drury & Rollins	"vars. *borealis, koliana, jordalii, villosa*"	*S. borealis*	*S. borealis*		*Smelowskia borealis*
S. brevicaulis Steud.					*Hornungia alpina*
S. californica A. Gray					*Descurainia californica*
S. calycina (Stephen) C. A. Mey.		*S. calycina*	*S. calycina*	*S. calycina*	*Smelowskia calycina*
S. cinerea C. A. Mey.					*Smelowskia alba*
S. cordifolia Walp.					*Eutrema cordifolium*
S. flavissina Kar. & Kir.					*Sophiopsis flavissima*
S. fremontii S. Watson	*Polyctenium fremontii*				*Polyctenium fremontii*
S. holmgrenii Rollins	*S. holmgrenii*	*S. holmgrenii*	*S. holmgrenii*		*Smelowskia holmgrenii*
S. inopinata (Korn.) Korn.		*S. inopinata*		*S. inopinata*	*Smelowskia inopinata*
S. integrifolia C. A. Mey.					*Eutrema integrifolium*
S. johnsonii G. A. Mulligan	*S. borealis* var. *jordalii*				*Smelowskia johnsonii*
S. jurtzevii Velichkin			*S. jurtzevii*	*S. porsildii*	*Smelowskia porsildii*
S. koelzii (Rech.f.) Rech.f.		*S. calycina*	*S. koelzii*	*S. calycina*	*Smelowskia calycina*
S. linearilobα Rydb.	*S. calycina* var. *americana*		*S. linearilobα*		*Smelowskia americana*
S. lobata Rydb.	*S. calycina* var. *americana*		*S. lobata*		*Smelowskia americana*
S. media (W. H. Drury & Rollins) Velichkin	*S. calycina* var. *media*		*S. media*		*Smelowskia media*
S. mongolica (Korn.) N. Busch		*S. mongolica*		*Hedinia mongolica*	*Hedinia mongolica*
S. ovalis M. E. Jones	"vars. *ovalis, congesta*"	*S. ovalis*	*S. ovalis*		*Smelowskia ovalis*
S. parryoides (Cham.) Polunin				*Ermania parryoides*	*Ermania parryoides*
S. parviflora Walp.					*Eutrema edwardsii*
S. pectinata (Bunge) Velichkin			*S. pectinata*	*S. pectinata*	*Smelowskia pectinata*
S. porsildii (W. H. Drury & Rollins) Jurtzev	*S. calycina* var. *porsildii*		*S. porsildii*	*S. porsildii*	*Smelowskia porsildii*
S. pyriformis W. H. Drury & Rollins	*S. pyriformis*	*S. pyriformis*			*Smelowskia pyriformis*
S. sisymbrioides B. Fedtsch.					*Sophiopsis sisymbrioides*
S. spathulatifolia Velichkin	*S. calycina* var. *integrifolia*		*S. spathulatifolia*		*Smelowskia americana*
S. tianschanica Velichkin			*S. tianschanica*	*S. tianschanica*	*Smelowskia calycina*
S. tibetica (Thomson) Lipsky					*Hedinia tibetica*
S. tilingii (Regel) V. N. Voroshilov				*S. tilingii*	*Smelowskia inopinata*

Rech. f.) to *S. koelzii*, which was later treated as a synonym of *S. calycina* by Hedge (1968).

In a worldwide treatment of *Smelowskia*, Velichkin (1979) recognized seven Asian species (*S. alba*, *S. bifurcata*, *S. calycina*, *S. jurtzevii*, *S. koelzii*, *S. pectinata*, and *S. tianschanica*) and seven North American species (*S. americana*, *S. linearilobа*, *S. lobata*, *S. media*, *S. ovalis*, *S. porsildii*, and *S. spathulatifolia*). Rollins (1993) recognized five North American species of *Smelowskia*, *S. borealis* (4 varieties), *S. calycina* (4 varieties), *S. holmgrenii*, *S. ovalis* (2 varieties), and *S. pyriformis*. Mulligan (2001) recently recognized two additional species, *S. johnsonii* (formerly *S. borealis* var. *jordalii* W. H. Drury & Rollins) and *S. media* (formerly *S. calycina* var. *media* W. H. Drury & Rollins). However, Mulligan's (2001) new combination of *S. media* is illegitimate because of its earlier use by Velichkin (1979).

The purpose of the present study was twofold: first, to test the monophyly of *Smelowskia* as delimited by Drury and Rollins (1952), Botschantzev (1968), Velichkin (1979), Rollins (1993), and Czerepanov (1995) (Table 2), with emphasis on North American versus Asian taxa; second, to test the relationship of *Smelowskia* with the North American genus *Polyctenium* and putatively related genera. Relationships to *Smelowskia* have been suggested for *Descurainia* Webb & Berthel., *Redowskia*, and *Sophioposis* by Schulz (1924, 1936), *Ermania* by Drury and Rollins (1952), *Hedinia* Ostenf. by Velichkin (1979), and *Sinosophiopsis* Al-Shehbaz and *Gorodkovia* Botsch. & Karav. by Al-Shehbaz (pers. obs.). For comparative morphology of these nine genera, see Table 1. Sequence comparisons of the internal transcribed spacers of nuclear ribosomal DNA and the 5.8S rRNA gene (collectively, ITS region) and the *trn*L intron region of the chloroplast genome were used to assess evolutionary relationships and taxonomic treatments of *Smelowskia*. ITS sequence data are the most widely used nuclear regions in phylogenetic analyses within families (Baldwin et al., 1995). Examples in the Brassicaceae include *Arabidopsis* (DC.) Heynh. (O'Kane et al., 1997; Koch et al., 1999a; Al-Shehbaz & O'Kane, 2002; O'Kane & Al-Shehbaz, 2003), *Brassica* L. and other genera (Yang et al., 1999), *Cardamine* L. (Franzke et al., 1998), *Caulanthus* S. Watson and *Streptanthus* Nutt. (Pepper & Norwood, 2001), *Cochlearia* L. (Koch et al., 1999b), *Crambe* L. (Francisco-Ortega et al., 1999), *Draba* L. (Koch & Al-Shehbaz, 2002), *Halimolobus* Tausch and related genera (Bailey et al., 2002), *Lepidium* L. (Bowman et al., 1999), *Pachyphragma* (DC.) Rchb. and *Gagria* M. Král (Mummenhoff et al., 2001a), *Sisymbrium* L. (Warwick et al., 2002), *Thlaspi* L. (Koch & Mummenhoff, 2001), *Vella* L. (Crespo et al., 2000), and *Yinshania* Ma & Y. Z. Zhao (Koch & Al-Shehbaz, 2000). The *trn*L intron sequence data also have potential phylogenetic utility for *Cardamine* L. and *Dentaria* L. (Sweeney & Price, 2000), *Cochlearia* (Koch et al., 1999b), *Lepidium* and *Cardaria* (Mummenhoff et al., 2001b), *Rorippa* Scop. (Bleeker et al., 2002), and *Sphaerocardamum* S. Schauer and related genera (Bailey & Doyle, 1999).

Materials and Methods

Plant material

Leaves (100 mg or less) were sampled from herbarium specimens or silica-gel dried samples of field-collected material (Table 3). Where possible, multiple accessions were assessed for each species. Ingroup species were selected based on available material and to represent the morphological and geographical diversity of *Smelowskia* and/or related genera. ITS sequences (Table 3) were obtained from 15 taxa (13 species) of *Smelowskia* (65 accessions) and 13 species (23 accessions) from the purported related genera *Descurainia* (*D. californica* (A. Gray) O. E. Schulz, *D. pinnata* (Walter) Britton, *D. sophia* (L.) Webb), *Ermania* (*E. parryoides* (Cham.) Botsch.), *Gorodkovia* (*G. jacutica* Botsch. & Karav.), *Hedinia* (*H. tibetica* (Thomson) Ostenf.), *Polyctenium* (*P. fremontii* (S. Watson) Greene and *P. williamsiae* Rollins), *Redowskia* (*R. sophiifolia* Cham. & Schltdl.), *Sinosophiopsis* (*S. bartholomewii* Al-Shehbaz), and *Sophioposis* (*S. annua* (Rupr.) O. E. Schulz, *S. flavissima* (Kar. & Kir.) O. E. Schulz, *S. sisymbrioides* (Regel & Herder) O. E. Schulz). The *trn*L intron sequences (Table 3) were obtained for 13 species of *Smelowskia* (25 accessions) and 13 species (17 accessions) from the above genera.

Five outgroup taxa were initially included in both the ITS and *trn*L analyses. Selection of an appropriate outgroup(s) was difficult, since with the exception of the tribe Brassiceae, all other tribes in the family are not believed to represent natural groups. Representatives of two subtribes of Sisymbrieae (sensu Schulz, 1936) were included as outgroups, i.e., *Arabidopsis thaliana* (L.) Heynh. (Arabidopsidinae) and *Sisymbrium irio* L. (Sisymbrinae), along with representatives of three other tribes: *Arabis alpina* L. (Arabideae), *Brassica rapa* L. (Brassiceae), and *Capsella bursa-pastoris* (L.) Medik. (Lepidieae, Capsellinae). The ITS sequences of *Arabidopsis thaliana*, *Arabis alpina*, *B. rapa*, *C. bursa-pastoris*, and *S. irio* and the *trn*L sequences of the first two were obtained from GenBank (Ta-

Table 3. Taxa sequenced for ITS region and *trn*L intron.

Accession No. and taxon	Collection (herbarium*)	Geographic origin	GenBank accession No. ITS	GenBank accession No. *trn*L
Tribe Sisymbrieae				
Subtribe Descurainiinae				
Smelowskia				
1. *S. alba*	27 June 1961, *Sergieskaia s.n.* (DAO)	Russia	AY230561	AY230533
2. *S. alba*	27 July 1967, *Egorova & Siplivinsky s.n.* (LE)	Russia	AY230562	—
3. *S. alba*	1968, *Egorova & Siplivinsky s.n.* (LE)	Russia	AY230563	—
4. *S. americana*	*Parmelee 4285a* (DAO)	Canada (AB)	AY230584	AY230522
5. *S. americana*	*de Vries 2231-64* (DAO)	Canada (AB)	AY230635	—
6. *S. americana*	*Calder 37261* (DAO)	Canada (AB)	AY230636	—
7. *S. americana*	*Taylor et al. 3210* (DAO)	Canada (BC)	AY230638	—
8. *S. americana*	*Taylor & Ferguson 2349* (DAO)	Canada (BC)	AY230639	—
9. *S. americana*	*Stein & Neill 1804* (MO)	U.S.A. (CO)	AY230575	—
10. *S. americana*	*Hultén & Weber 11081* (DAO)	U.S.A. (CO)	AY230580	—
11. *S. americana*	*Beaman & Stone 1646* (DAO)	U.S.A. (MT)	AY230637	—
12. *S. americana*	*Tiehm 9856* (DAO)	U.S.A. (NV)	AY230583	AY230521
13. *S. americana*	*Batten 97-7* (ALA)	U.S.A. (UT)	AY230579	—
14. *S. americana*	*Beaman & Stone 1461* (DAO)	U.S.A. (UT)	AY230582	—
15. *S. americana*	*Douglas & Douglas 3825* (DAO)	U.S.A. (WA)	AY230596	—
16. *S. americana*	*Gillet & Taylor 11667* (DAO)	U.S.A. (WY)	AY230634	—
17. *S. bifurcata*	*Khanmenchun et al. 1401* (LE)	Russia	AY230603	AY230560
18. *S. borealis* var. *borealis*	*Cody 17063* (DAO)	Canada (NT)	AY230633	—
19. *S. borealis* var. *borealis*	*Cody 17180* (DAO)	Canada (NT)	AY230570	—
20. *S. borealis* var. *borealis*	*Cody & Ginns 33864* (DAO)	Canada (YK)	AY230632	AY230528
21. *S. borealis* var. *borealis*	*Calder & Gillet 25931* (DAO)	Canada (YK)	AY230572	AY230529
22. *S. borealis* var. *borealis*	*Parker 1094* (ALA)	Canada (YK)	AY230565	—
23. *S. borealis* var. *borealis*	*Roland 3203* (ALA)	U.S.A. (AK)	AY230564	AY230530
24. *S. borealis* var. *borealis*	*Lipkin & Cook 93-88* (DAO)	U.S.A. (AK)	AY230568	AY230532
25. *S. borealis* var. *borealis*	*Viereck 1381* (ALA)	U.S.A. (AK)	AY230574	—
26. *S. borealis* var. *borealis*	*Viereck & Jones 5766* (ALA)	U.S.A. (AK)	AY230569	—
27. *S. borealis* var. *koliana*	*Murray 4171* (ALA)	U.S.A. (AK)	AY230566	—
28. *S. borealis* var. *koliana*	*Batten 49* (ALA)	U.S.A. (AK)	AY230567	—
29. *S. borealis* var. *koliana*	*Murray 8582* (DAO)	U.S.A. (AK)	AY230571	—

Table 3. Continued.

Accession No. and taxon	Collection (herbarium*)	Geographic origin	GenBank accession no. ITS	GenBank accession no. *trn*L
30. *S. calycina*	*Anonymous 3179* (HNWP)	China	AY230641	—
31. *S. calycina*	*Sultanov & Junusor 986* (LE)	Russia	AY230581	—
32. *S. calycina*	*Parker 4056* (DAO)	Russia	AY230588	AY230527
33. *S. calycina*	*Parker 4056* (ALA)	Russia	AY230589	—
34. *S. calycina*	*Gysev 5960* (LE)	Tajikistan	AY230640	—
35. *S. calycina*	*Lukanenkova 213* (LE)	Tajikistan	AY230576	AY230523
36. *S. holmgrenii*	*Goodrich 11970* (GH)	U.S.A. (NV)	AY230598	AY230555
37. *S. holmgrenii*	*Goodrich 11970* (GH)	U.S.A. (NV)	AY230599	—
38. *S. holmgrenii*	*Holmgren & Ballenger 7076* (GH)	U.S.A. (NV)	AY230628	AY230557
39. *S. holmgrenii*	11 July 1979, *Goodrich s.n.* (GH)	U.S.A. (NV)	AY230629	AY230556
40. *S. inopinata*	*Kharkevich & Buch 317B* (MO)	Russia	AY230600	AY230536
41. *S. inopinata*	*Pimenov & Stephanovych 198* (LE)	Russia	AY230601	—
42. *S. johnsonii*	*Viereck & Bucknell 4102* (ALA)	U.S.A. (AK)	AY230573	AY230531
43. *S. johnsonii*	*Johnson et al. 688* (DAO)	U.S.A. (AK)	AY230630	AY230538
44. *S. johnsonii*	*Johnson et al. 688* (ALA)	U.S.A. (AK)	AY230631	AY230539
45. *S. media*	*Cody & Johannson 12876* (DAO)	Canada (NT)	AY230643	—
46. *S. media*	*Calder 34367* (DAO)	Canada (YK)	AY230587	—
47. *S. media*	*Code 27207* (DAO)	Canada (YK)	AY230642	—
48. *S. media*	*Murray 6901* (DAO)	U.S.A. (AK)	AY230586	AY230520
49. *S. media*	*LePage 23826* (DAO)	U.S.A. (AK)	AY230585	AY230519
50. *S. media*	*Parker et al. 9275* (ALA)	U.S.A. (AK)	AY230578	—
51. *S. media*	*Parker et al. 7182* (DAO)	U.S.A. (AK)	AY230590	AY230526
52. *S. ovalis* var. *ovalis*	*Pinder-Moss & Pojar 1006* (DAO)	Canada (BC)	AY230594	AY230534
53. *S. ovalis* var. *ovalis*	*St. Jones 4839* (MO)	U.S.A. (WA)	AY230597	—
54. *S. ovalis* var. *congesta*	*Gillett 350* (DAO)	U.S.A. (CA)	AY230595	—
55. *S. pectinata*	*Velychnin N495* (LE)	Russia	AY230604	AY230535
56. *S. porsildii*	*Parker 7575* (ALA)	U.S.A. (AK)	AY230577	AY230524
57. *S. porsildii*	*Murray 3941* (MO)	U.S.A. (AK)	AY230592	—
58. *S. porsildii*	11 July 1959, *Johnson et al. s.n.* (DAO)	U.S.A. (AK)	AY230591	—
59. *S. porsildii*	*Murray 6884* (DAO)	U.S.A. (AK)	AY230623	AY230525
60. *S. porsildii*	25 June 1970, *Katenin et al. s.n.* (DAO)	Russia	AY230624	—
61. *S. porsildii*	1972, *Zhukova & Jurtzev s.n.* (LE)	Russia	AY230593	—
62. *S. pyriformis*	*Parker & Blank 9012* (ALA)	U.S.A. (AK)	AY230602	AY230537

Table 3. Continued.

Accession No. and taxon	Collection (herbarium*)	Geographic origin	GenBank accession no. ITS	GenBank accession no. *trn*L
63. *S. pyriformis*	*Parker & Blank 9012* (MO)	U.S.A. (AK)	AY230648	—
64. *S. pyriformis*	*Parker 664* (ALA)	U.S.A. (AK)	AY230644	—
65. *S. pyriformis*	*Parker 610* (ALA)	U.S.A. (AK)	AY230645	—
66. *Descurainia californica*	*Howell et al. 54448* (MO)	U.S.A. (CA)	AY230616	AY230544
67. *D. californica*	*Tiehm & Tucker 6713* (MO)	U.S.A. (NV)	AY230617	AY230545
68. *D. pinnata*	*Koch 77536* (DAO)	Mexico	AY230620	AY230543
69. *D. pinnata*	*Reznicek & Catling 5523* (DAO)	Canada (ON)	AY230621	—
70. *D. pinnata*	*Boivin & Perron 12847* (DAO)	Canada (MB)	AY230622	—
71. *D. sophia*	*Russell S52274* (DAO)	Canada (SK)	AY230618	AY230546
72. *D. sophia*	*Thomas 1269* (DAO)	Canada (SK)	AY230619	AY230547
73. *Ermania parryoides*	*Parker & Zagrebin 6047* (ALA)	Russia	AY230625	AY230540
74. *E. parryoides*	*Parker 4170* (ALA)	Russia	AY230626	AY230541
75. *Gorodkovia jacutica*	*Kalydshuriski 75/1* (LE)	Russia	AY230606	AY230548
76. *G. jacutica*	*Elias & Murray 11462* (ALA)	Russia	AY230646	—
77. *G. jacutica*	*Elias & Murray 11352* (ALA)	Russia	AY230605	AY230549
78. *Hedinia tibetica*	*Ho et al. 1033* (MO)	China	AY230607	—
79. *H. tibetica*	*Hurka 99-0505-50-00* (no herbarium)	Tajikistan	AY230627	AY230551
80. *Polyctenium fremontii*	*Cronquist 8207* (DAO)	U.S.A. (OR)	AY230613	—
81. *P. fremontii*	*Tiehm et al. 11703* (DAO)	U.S.A. (CA)	AY230647	—
82. *P. fremontii*	*Ondricek 59* (MO)	U.S.A. (CA)	AY230614	AY230558
83. *P. williamsiae*	*Rollins & Rollins 83219* (MO)	U.S.A. (NV)	AY230615	AY230559
84. *Redowskia sophiifolia*	*Geonova 148* (LE)	Russia	AY230608	AY230542
85. *Sinosophiopsis bartholomewii*	*Ho et al. 3000* (MO)	China	AY230609	AY230550
86. *Sophiopsis annua*	*Anonymous 870473* (HNWP)	China	AY230610	AY230552
87. *S. flavissima*	12 June 1959, *Goloskokov s.n.* (LE)	Kazakhstan	AY230611	AY230554
88. *S. sisymbrioides*	*Egorova 2349* (LE)	Tajikistan	AY230612	AY230553
Initial Outgroup				
89. *Arabidopsis thaliana*	O'Kane et al. (1997)		U43225	X74573
90. *Arabis alpina*	O'Kane and Al-Shehbaz, unpublished data		AF137559	AY034180
91. *Brassica rapa*	Warwick et al. (2002)		AF531563	AY236217
92. *Capsella bursa-pastoris*	Warwick et al. (2002)		AF531561	AY236218
93. *Sisymbrium irio*	Warwick et al. (2002)		AF531558	AY236216

ble 3). Initial analyses showed that if the above five species were included in the outgroup, the ingroup was not monophyletic, as *Arabidopsis* (DC.) Heynh. and *Capsella* Medik. formed part of the ingroup. Subsequent analyses included these five taxa, with only *Arabis*, *Brassica*, and *Sisymbrium* assigned to the outgroup.

DNA EXTRACTION

DNA was extracted from approximately 100 mg or less of dried leaf tissue using Bio 101 FastDNA Kit (Qbiogene Inc., Carlsbad, CA, U.S.A.) following manufacturer's instructions. The final elution was performed in 80 µl of DES, and then brought to 10 mM Tris (8.0) by the addition of 1/10th volume of 100 mM Tris (pH 8.0).

ITS REGION OF NUCLEAR RIBOSOMAL DNA

The entire ITS region (including internal transcribed spacers ITS1 and ITS2 of nuclear ribosomal DNA and the 5.8S rRNA gene) was amplified as a single unit using primers ITS1–18S described in O'Kane et al. (1997) and ITS4 described in White et al. (1990). The amplifications were performed using Ready-To-Go PCR Beads (Amersham Biosciences, Piscataway, NJ, U.S.A.) and 2.0 µl of diluted genomic DNA in a total of 25 µl. Amplifications were performed on a Thermolyne Amplitron thermocycler (Techne Inc., Princeton, NJ, U.S.A.) using an initial denaturing step of 95°C for 3 min.; 35 cycles of 95°C for 35 sec., 48°C for 35 sec., and 70°C for 1 min.; and a final extension at 72°C for 10 min. The PCR reaction was run on a 1.0% TBE NuSieve (Biowhittaker Molecular Applications, Rockland, ME, U.S.A.) agarose gel followed by band excision and purification using the GFX-PCR DNA and Gel Band Purification Kit (Amersham Biosciences).

Direct sequencing using fluorescently labeled primers (ITS1–18S and ITS4) was performed by Canadian Molecular Research Services (Ottawa, ON, Canada) on a LICOR automated sequencer. Base readings for both forward and reverse sequences as well as an edited alignment for each sample were verified with associated chromatograms. The ITS1 and ITS2 sequences of accessions 3, 26, 37, 53, and 61 (Table 3) were obtained following the protocol given in Mummenhoff et al. (1997).

*trn*L INTRON

The *trn*L intron was amplified using the c and d primers described in Taberlet et al. (1991). The PCR reactions used Ready-To-Go PCR Beads (Amersham Biosciences) and 0.2 µl of genomic DNA in a total of 25.0 µl. Amplifications were performed on a Thermolyne amplitron thermocycler (Techne Inc., Princeton, NJ, U.S.A.) using an initial denaturing step of 94°C for 3 min.; 35 cycles of 95°C for 1 min., 50° for 45 sec., and 72° for 45 sec.; and a final extension at 72° for 10 min. The PCR reaction was run on a 1.0% TBE NuSieve (Biowhittaker Molecular Applications) agarose gel followed by purification with the GFX PCR DNA and Gel Band Purification Kit (Amersham Biosciences).

Direct sequencing was carried out on a LICOR automated sequencer using the DYEnamic Direct cycle sequencing kit with 7-deaza-dGTP (Amersham Biosciences) and with fluorescently labeled primers c and d. Both forward and reverse images were captured and base-called with E-Seq (LiCor, Lincoln, NE, U.S.A.) software. Forward and reverse sequences for individual samples were aligned and edited using AlignIR (Licor).

DATA SCORING AND ANALYSIS

The sequences were automatically assembled using the software ASSEMBLYLIGN (Kodak, Newhaven, CT, U.S.A.) and aligned using clustal in MEGALIGN (DNA Star, Madison, WI, U.S.A.) and further aligned by eye. For ITS, insertions/deletions (indels), all of which appeared in either ITS1 or ITS2, were treated as missing data in accessions lacking the sequence, with the exception of a 16 bp indel in ITS1. The latter indel formed part of a 19 bp region that was excluded from the analysis. This approach retains phylogenetic information from taxa not missing data at the indel. Boundaries of the ITS1 and ITS2 regions were determined by comparison with the published sequences of *Arabidopsis thaliana* (O'Kane et al., 1997), *Sisymbrium altissimum* L. (Francisco-Ortega et al., 1999), and *Sisymbrium irio* (Warwick et al., 2002). It has been previously shown that indels in the *trn*L intron provide reliable phylogenetic resolution (Mummenhoff et al., 2001b). Therefore, we treated insertions/deletions (indels) as missing data, and those indels of 2 bp and greater (10 indels in total) were treated as separate characters in the analysis and scored for presence/absence.

Maximum parsimony analyses of the aligned sequences of ITS and *trn*L were conducted separately using the computer program PAUP*, version 4.0b2 (Swofford, 1999). For the ITS sequence data, the most parsimonious trees were generated using the heuristic search algorithm, which employed tree bi-

section-reconnection (TBR) branch-swapping, equal weighted characters, with gaps treated as missing data, with 25,000 random additions of the sampled taxa, with 20 trees saved per replicate. Limitations of computer memory required constraining maximum tree number at 40,000. A second heuristic search was conducted using the 50% majority-rule tree obtained in the above analysis as the starting tree and the replicate allowed to swap to completion using the TBR option. Statistics relating to the amount of homoplasy in the trees, described in PAUP*, were obtained for each tree and a strict consensus tree was computed for each of the two heuristic analyses. A third heuristic search on the ITS sequence data was conducted where *Smelowskia* was constrained to monophyly using the constraints function in PAUP*, i.e., 2000 replicates with random addition of taxa, TBR swapping, and a maximum of 20 trees per replicate. Two statistical tests available in PAUP*, the parametric Kishino-Hasegawa and the nonparametric Templeton (Wilcoxon signed ranks) and winning-sites tests, were used to evaluate the difference in length between single most parsimonious trees from each of the two analyses. For the *trn*L sequence data, the most parsimonious trees were generated using the heuristic search algorithm, which employed TBR branch-swapping, equal weighted characters, with gaps 2 bp or less treated as missing data and gaps greater than 2 bp in length treated as separate characters (scored presence/absence), with 10,000 random additions of the sampled taxa, with 1000 trees saved per replicate. In addition, a heuristic search on the *trn*L sequence data was conducted where *Smelowskia* was constrained to monophyly using the constraints function in PAUP*, i.e., 10,000 replicates with random addition of taxa, TBR swapping, and a maximum of 100 trees per rep.

The ITS and *trn*L sequence data were combined for 47 accessions for which *trn*L data was available. In order to test whether the data sets were congruent and could be combined, heterogeneity among each data set was assessed using the partition homogeneity test (Farris et al., 1995) as implemented in PAUP. No significant heterogeneity was detected ($P = 0.52$), indicating that the two data sets could be combined. The most parsimonious trees were generated using the heuristic search algorithm, which employed TBR branch-swapping, with equal weighted characters, with gaps treated as missing data for ITS, and for *trn*L gaps 2 bp or less were treated as missing data and gaps greater than 2 bp in length treated as separate characters (scored presence/absence), with 25,000 random additions of the sampled taxa, with 20 trees saved per replicate.

For the ITS, *trn*L, and combined ITS/*trn*L sequence data, 100, 500, and 500 bootstrap (Felsenstein, 1985) replicates, respectively, were generated in PAUP* using a full heuristic search, with options ACCTRAN, MULTREES = MULPARS, and TBR, and each replicate generated with simple addition sequence of taxa, in order to test the stability of particular nodes in the parsimony analyses. Limitations of computer memory required constraining the maximum number of trees to 400 per replicate. Pair-wise distance sequence divergence of ITS and *trn*L were calculated for each accession pair in PAUP* using the Kimura two parameter model (Kimura, 1980) and the pair-wise deletion option for gaps and ambiguous data.

Results and Discussion

ITS sequence data

A total of 36 taxa (93 accessions) was included in the analysis (Table 3), 5 of which were included in the outgroup. The resulting multiple alignment of the internal transcribed spacer (ITS) region, including 5.8S gene, was 644 bp long. Sequences are deposited in GenBank (accession numbers in Table 3), and the full alignment is available from the first author. One region of ITS1 (19 bp) was difficult to align and was excluded from the analyses (bases 109 to 127). For the remaining 625 characters, 389 base positions were constant and uninformative, 81 were variable but not parsimony informative, and 155 were potentially parsimony informative. The ITS1 and ITS2 regions exhibited similar amounts of variation, with 129 variable in 260 sites (50%) for ITS1 and 99 variable in 201 sites (49%) for ITS2. Only 8 of the 164 sites (5%) in the 5.8S gene showed any variation.

The sequence alignment required the introduction of 13 indels in ITS1 and 11 indels in ITS2. Most indels were 1, 2, or 3 bp. However, a 7 bp deletion in ITS1 was detected in *Brassica rapa*, and appears to be the same 10 bp deletion described for its sister species *B. oleracea* L. by Francisco-Ortega et al. (1999). A 16 bp deletion occurred in the 19 bp ITS1 region that was excluded from the analyses and is the same 16 bp deletion reported for *Sisymbrium altissimum* by Francisco-Ortega et al. (1999) and other Old World *Sisymbrium* taxa (Warwick et al., 2002).

Among the ingroup taxa, the longest ITS region (609 bp, excluding indels) occurred in *Smelowskia holmgrenii* and the shortest (581 bp, excluding indels) in *Hedinia tibetica*. The G + C content of taxa within the ingroup was similar, with an average value of 55.9%.

Conspecific accessions of several species of *Smelowskia*, *Descurainia*, *Gorodkovia*, and *Polyctenium* had identical sequences over the entire length of the ITS alignment; these are indicated in parentheses after the species name in Figures 1 and 2. Identical sequences were also detected for some *Smelowskia* species (Fig. 2). For example, two accessions of *S. borealis* var. *koliana* (acc. 28, 29) had identical sequences to *S. media* (acc. 49–51).

ITS sequence divergence (excluding ambiguities) among conspecific accessions was usually small: *Smelowskia alba* (3 acc., range 0.17–0.34%), *S. americana* (13 acc., 0–0.85%), *S. borealis* var. *borealis* (9 acc., 0–3.10%), *S. borealis* var. *koliana* (Gombócz) W. H. Drury & Rollins (3 acc., 0–0.17%), *S. calycina* (6 acc., 0–3.23%), *S. holmgrenii* (4 acc., 0–0.67%), *S. inopinata* (2 acc., 0%), *S. johnsonii* (3 acc., 0–0.17%), *S. media* (7 acc., 0–0.67%), *S. porsildii* (6 acc., 0–0.84%), *S. pyriformis* (4 acc., 0%), *Descurainia californica* (2 acc., 0%), *D. pinnata* (3 acc., 0–1.35%), *D. sophia* (2 acc., 0%), *Ermania parryoides* (2 acc., 0.33%), *Gorodkovia jacutica* (3 acc., 0–0.50%), *Hedinia tibetica* (2 acc., 1.39%), and *Polyctenium fremontii* (3 acc., 0%).

The equal weight maximum parsimony analysis, which excluded autapomorphies, yielded 19,507 most parsimonious trees of 417 steps, with *Arabidopsis thaliana*, *Arabis alpina*, *Brassica rapa*, *Capsella bursa-pastoris*, and *Sisymbrium irio* as the outgroup taxa. When the 50% majority-rule tree of the above 19,507 trees was used as the starting tree in a subsequent heuristic search and then swapped to completion, a total of 19,739 most parsimonious trees was obtained. Homoplasy in the data set is low as measured by a consistency index (CI) of 0.54 and retention index (RI) of 0.79. The strict consensus tree from the two analyses was the same. Figure 1 shows the strict consensus tree of the 19,739 most parsimonious trees with bootstrap values, and Figure 2 shows one of the most parsimonious trees with branch lengths. Four major ingroup clades were evident: *Smelowskia* s.l. (*Smelowskia* s. str. and the related genera *Ermania*, *Gorodkovia*, *Hedinia*, *Redowskia*, *Sinosophiopsis*, and *Sophiopsis*), Holmgrenii (*Smelowskia holmgrenii*), *Polyctenium*, and *Descurainia* spp. *Descurainia* was clearly distinct from the rest of the genera included in the ingroup.

*trn*L INTRON SEQUENCE DATA

A total of 25 *Smelowskia* accessions and 17 accessions from related genera were included in the analysis (Table 3), along with sequences from the 5 outgroup taxa. The resulting multiple alignment of the *trn*L intron was 513 bp long. Sequences are deposited in GenBank (accession numbers in Table 3), and the full alignment is available from the first author. A total of 431 base positions were constant and uninformative, 37 were variable but not parsimony informative and 45 were potentially parsimony informative. All *Smelowskia* accessions had a *trn*L intron length of 497 bp, with the exception of *S. holmgrenii* (492 bp, deletion 371–375 bp). The alignment required the introduction of 16 indels to either related genera or outgroup taxa. Five were 1 bp, 1 was a 2 bp indel, and 10 were greater than 2 bp. Two 7 bp deletions were observed in *Sophiopsis flavissima* (418–424 bp) and in *Sinosophiopsis bartholomewii* (188–194 bp). A 9 bp insertion (392–400 bp) was observed for the 2 *Polyctenium* species, thus increasing *trn*L intron length to 506 bp, the longest in the analysis. A unique deletion was observed for *S. holmgrenii* accessions (371–375 bp). A unique 5 bp deletion (114–118 bp) and a 59 bp deletion (229–288) were observed for *Descurainia californica* and *D. pinnata*, resulting in the shortest *trn*L intron lengths in the ingroup (434 bp). The latter deletion (plus 3 additional deletions of 193–228 bp, 289–370 bp, 376–383 bp) was also observed in 3 of the 5 outgroup taxa (*Arabis alpina*, *Brassica rapa*, and *Sisymbrium irio*). *Brassica rapa* and *Sisymbrium irio* both had a 10 bp deletion (121–130 bp). The 10 indels greater than 2 bp were treated as separate characters in the analysis, bringing the total number of parsimony informative characters to 55. The G + C content of taxa within the ingroup was similar, with an average value of 34.6%.

The following 16 accessions had identical *trn*L sequences: *Smelowskia alba* (acc. 1, as listed in Table 3 and Figures), *S. americana* (acc. 4, 12), *S. borealis* var. *borealis* (acc. 20, 24), *S. calycina* (acc. 32), *S. inopinata* (acc. 40), *S. johnsonii* (acc. 42), *S. media* (acc. 48, 49, 51), *S. pyriformis* (acc. 62), *Ermania parryoides* (acc. 73, 74), *Gorodkovia jacutia* (acc. 77), *Redowskia sophiifolia* (acc. 84). The two accessions (43 and 44) of *S. johnsonii* had identical sequences, as did accessions 71 and 72 of *Descurainia sophia*.

The equal weight maximum parsimony analysis, which excluded autapomorphies, yielded 20 most parsimonious trees of 76 steps, with *Arabidopsis thaliana*, *Arabis alpina*, *Brassica rapa*, *Capsella bursa-pastoris*, and *Sisymbrium irio* as the outgroup taxa. Homoplasy in the data set is low as measured by a CI value of 0.88 and an RI value of 0.96. Figure 3 shows the strict consensus tree of the 20 most parsimonious trees with bootstrap values, and Figure 4 shows one of the most parsimonious trees

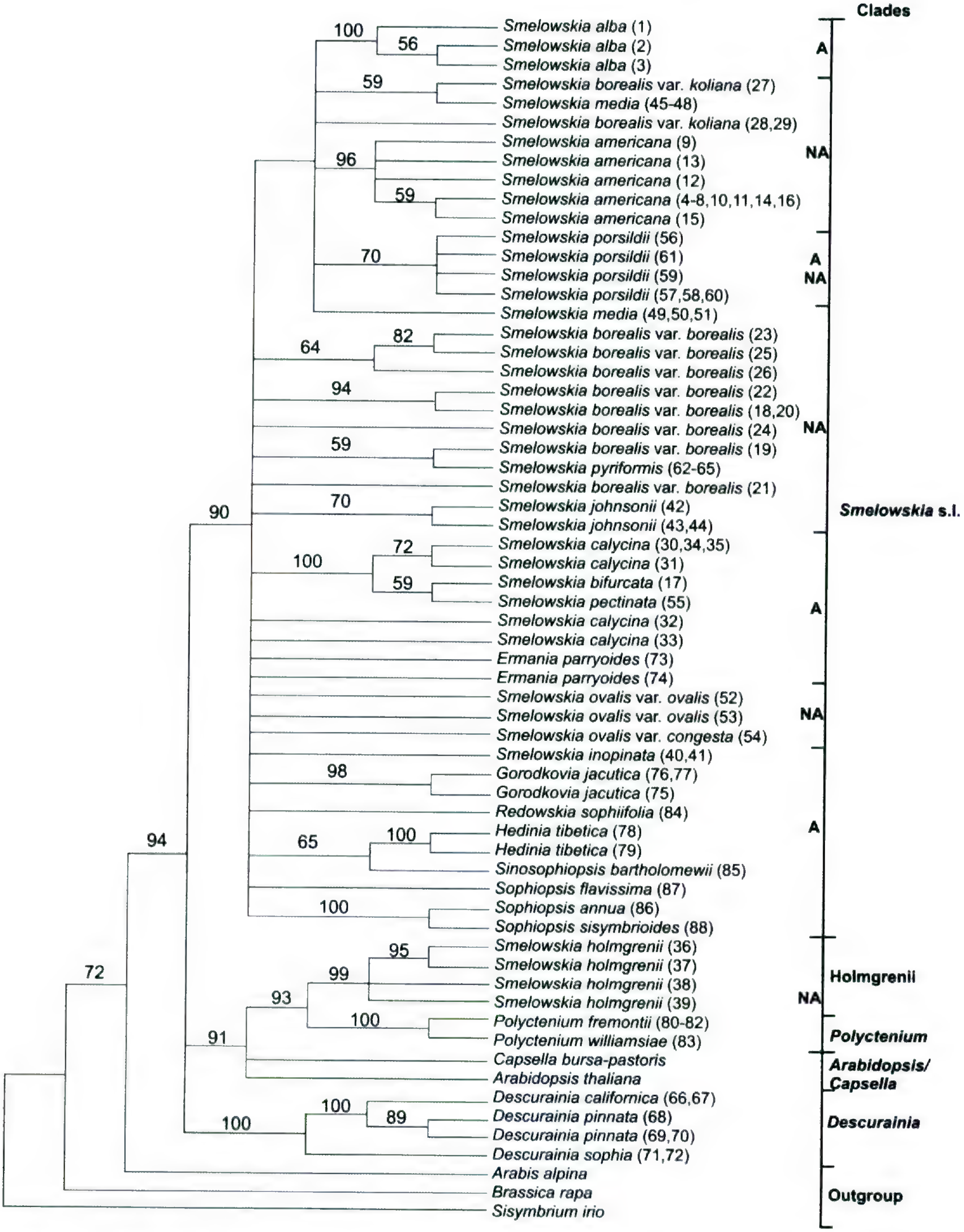


Figure 1. Strict consensus tree of 19,739 most parsimonious trees based on ITS sequences; tree length = 417 (excluding parsimony uninformative characters), CI = 0.54, RI = 0.79. Bootstrap values from 100 replicates appear above branches with > 50% bootstrap support. Accession number as listed in Table 3 is given in parentheses after the species name; all conspecific samples listed within parentheses had identical sequences. The four major clades (*Smelowskia* s.l. [i.e., *Smelowskia* and related genera *Ermania*, *Gorodkovia*, *Hedinia*, *Redowskia*, *Sinosophiopsis*, and *Sophiopsis*], *Polyctenium*, Holmgrenii, *Descurainia*) recognized in the analysis and the outgroup taxa are indicated to the right. Asian (A) versus North American (NA) distributions are indicated in bold for species in the ingroup.

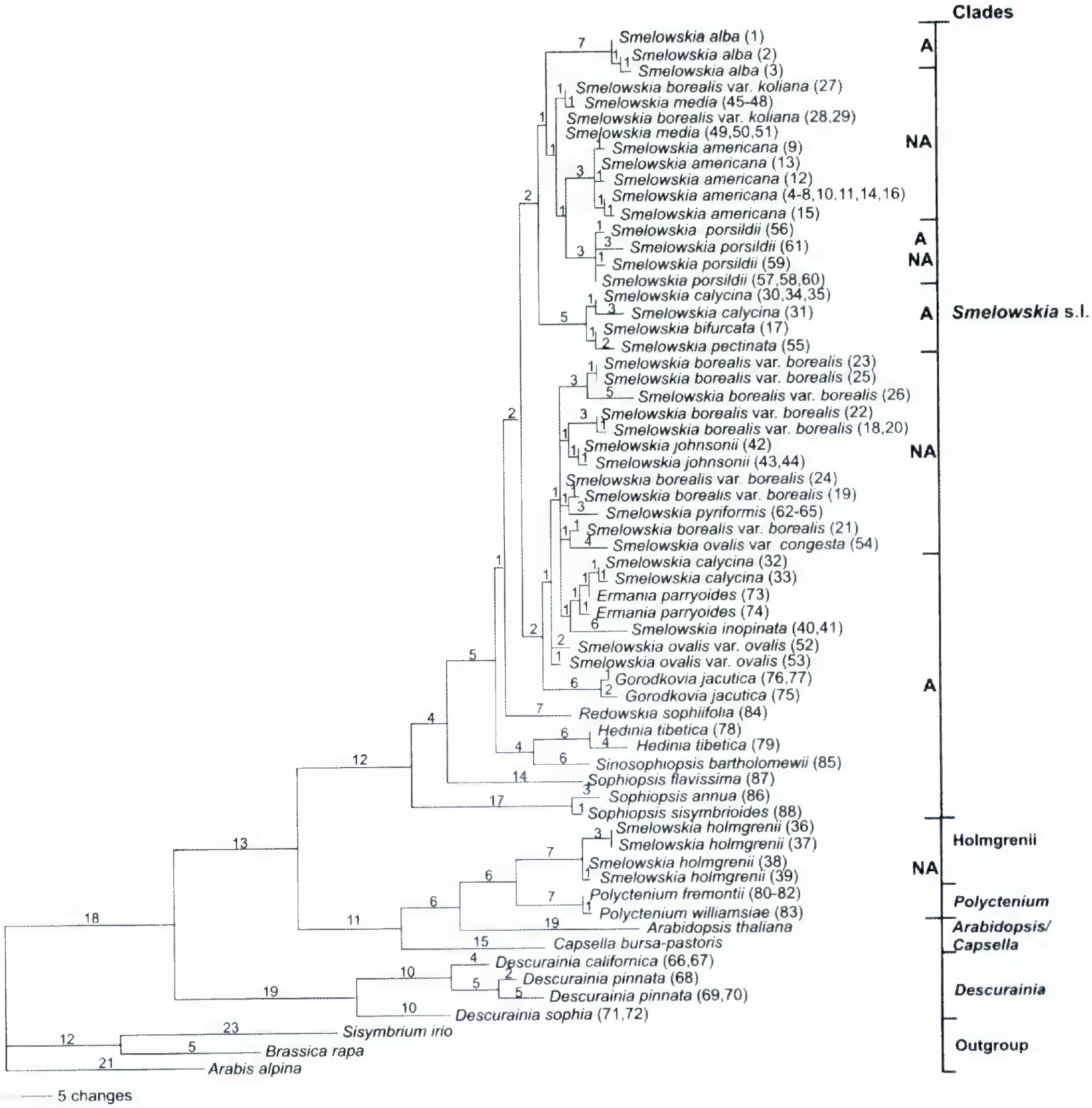
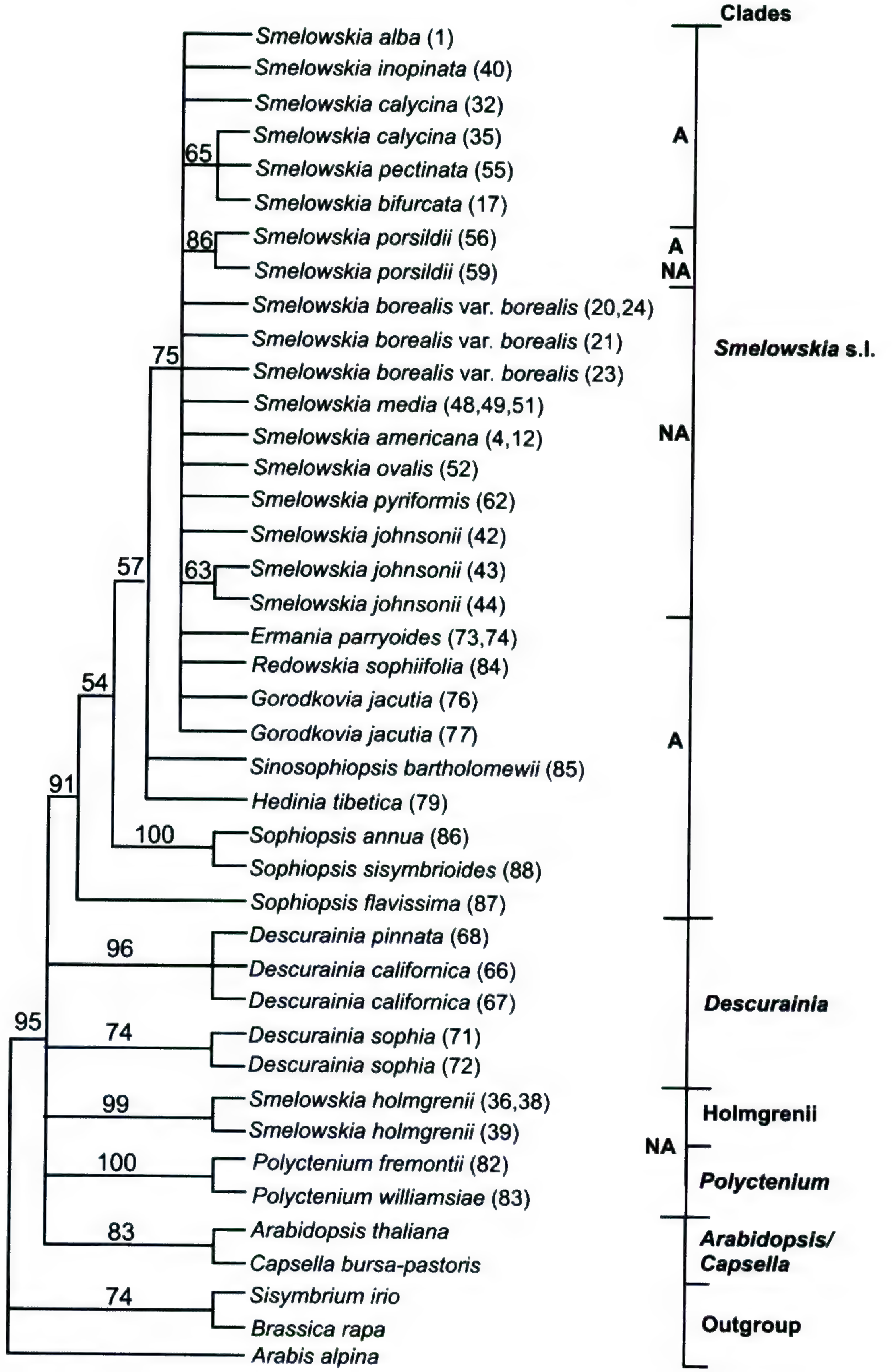


Figure 2. One of the most parsimonious trees based on ITS sequences; tree length = 417 (excluding parsimony uninformative characters), CI = 0.41, RI = 0.75. The number of characters supporting each clade is indicated. The four major clades (*Smelowskia* s.l., *Polyctenium*, Holmgrenii, *Descurainia*) recognized in the analysis and the outgroup taxa are indicated to the right. Asian (A) versus North American (NA) distributions are indicated in bold for species in the ingroup.

with branch lengths. Four major ingroup clades were evident: *Smelowskia* s.l. (*Smelowskia* s. str. and the related genera *Ermania*, *Gorodkovia*, *Hedinia*, *Redowskia*, *Sinosophiopsis*, and *Sophiopsis*), Holmgrenii, *Polyctenium*, and *Descurainia*. In contrast to the ITS data, the *trn*L data provided less than 50% bootstrap support (Fig. 3) for the clade containing the Holmgrenii, *Polyctenium* and *Arabidopsis/Capsella* subclades (Fig. 4).

ITS/*trn*L COMBINED SEQUENCE DATA

The combined ITS/*trn*L data set included 1143 characters; 830 were constant and uninformative, 112 were variable but not parsimony informative, and 201 were potentially parsimony informative. The equal weight maximum parsimony analysis, which excluded autapomorphies, yielded 896 most parsimonious trees of 461 steps, with *Arabidopsis thaliana*, *Arabis alpina*, *Brassica rapa*, *Capsella bursa-pastoris*, and *Sisymbrium irio* as the outgroup taxa. Homoplasy in the combined data set is low as measured by a CI value of 0.60 and an RI value of 0.81. Figure 5 shows the strict consensus tree of the 896 most parsimonious trees with bootstrap values, and Figure 6 shows one of the most parsimonious trees with branch lengths. Analysis of the


Clades
Smelowskia alba (1)
Smelowskia inopinata (40)
Smelowskia calycina (32)
Smelowskia calycina (35)
Smelowskia pectinata (55)
Smelowskia bifurcata (17)
Smelowskia porsildii (56)
Smelowskia porsildii (59)
Smelowskia borealis var. borealis (20,24)
Smelowskia borealis var. borealis (21)
Smelowskia borealis var. borealis (23)
Smelowskia media (48,49,51)
Smelowskia americana (4,12)
Smelowskia ovalis (52)
Smelowskia pyriformis (62)
Smelowskia johnsonii (42)
Smelowskia johnsonii (43)
Smelowskia johnsonii (44)
Ermania parryoides (73,74)
Redowskia sophiifolia (84)
Gorodkovia jacutia (76)
Gorodkovia jacutia (77)
Sinosophiopsis bartholomewii (85)
Hedinia tibetica (79)
Sophiopsis annua (86)
Sophiopsis sisymbrioides (88)
Sophiopsis flavissima (87)
Descurainia pinnata (68)
Descurainia californica (66)
Descurainia californica (67)
Descurainia sophia (71)
Descurainia sophia (72)
Smelowskia holmgrenii (36,38)
Smelowskia holmgrenii (39)
Polyctenium fremontii (82)
Polyctenium williamsiae (83)
Arabidopsis thaliana
Capsella bursa-pastoris
Sisymbrium irio
Brassica rapa
Arabis alpina
65
86
75
57
63
54
91
100
96
95
74
99
100
83
74
A
A
NA
Smelowskia s.l.
NA
A
Descurainia
Holmgrenii
NA
Polyctenium
Arabidopsis/
Capsella
Outgroup

combined data set yielded a topology that was nearly identical to that obtained from the analyses of the ITS data set, with either the same or slightly better bootstrap support. Four major ingroup clades were evident: *Smelowskia* s.l. (*Smelowskia* s. str. and the related genera *Ermania*, *Gorodkovia*, *Hedinia*, *Redowskia*, *Sinosophiopsis*, and *Sophiopsis*) (bootstrap support increased from 90 to 97%), Holmgrenii (*Smelowskia holmgrenii*), *Polyctenium*, and *Descurainia* spp. As in the ITS analysis, *S. holmgrenii* was very distinct from the *Smelowskia* s.l. clade and formed the sister clade to *Polyctenium*, although bootstrap support was reduced to 75% compared to 93% for ITS data.

Relationships and Circumscription of *Smelowskia*

1. *Smelowskia* s. str.

The ITS results indicate that *Smelowskia* sensu Schulz (1924, 1936) is not a monophyletic genus. *Smelowskia* species were split into two major clades, with *S. holmgrenii* (designated the "Holmgrenii" clade) forming a sister group to *Polyctenium*. The remaining *Smelowskia* taxa (*Smelowskia* s. str.) were included in a single clade (*Smelowskia* s.l.), along with other genera. The same pattern was apparent for the *trn*L sequence data. When *Smelowskia* was constrained to monophyly in separate analyses of the ITS and *trn*L data, using the constraints function in PAUP* and subjected to the same heuristic search as the unconstrained analysis, most parsimonious tree length increased by 43 steps from 417 to 460 steps for the ITS data and increased by 13 steps from 76 to 89 steps for the *trn*L data. These trees were highly significantly different in length ($P < 0.0001$) based on both the parametric Kishino-Hasegawa test and the nonparametric Templeton (Wilcoxon signed ranks) and winning-sites test.

The ITS- and *trn*L-based *Smelowskia* s. str. clade included *S. alba*, *S. americana*, *S. bifurcata*, *S. borealis*, *S. calycina*, *S. johnsonii*, *S. inopinata*, *S. media*, *S. ovalis*, *S. porsildii*, and *S. pyriformis*. With the exclusion of *S. holmgrenii*, the general ITS-based circumscription of *Smelowskia* s. str. basically follows Drury and Rollins (1952), Rollins (1993), and Velichkin (1979). The first two accounts are essentially identical, but Velichkin recognized additional North American species, all of which were treated by the other two authors as varieties or synonyms of *S. calycina* (Table 2). Velichkin depended extensively on the degree of development of nectar glands, abundance of simple versus branched trichomes, and shape of the septum to distinguish most species. However, these characters are so variable even sometimes within a population, that it is highly doubtful if they have any value in the separation of species and were, therefore, justifiably ignored by Drury and Rollins (1952).

Asian and North American species did not form separate clades. Based on ITS data, the Asian *Smelowskia* taxa were separated into three well-defined clades, each supported by a 100% bootstrap value (Fig. 1) and a fourth loosely supported clade (which occurred in 78% of the most parsimonious trees, but had a bootstrap value of less than 50%, and is thus not shown in Fig. 1). The first clade included three accessions of *S. alba*, the second two accessions of *S. inopinata*, and the third *S. calycina* (4 accessions), *S. bifurcata*, and *S. pectinata*. The fourth clade contained two accessions of *S. calycina* and *Ermania parryoides*. *Smelowskia pectinata* and *S. bifurcata* were sister taxa, separated by only two steps. Morphologically they are also very similar, differing primarily in leaf segment width, which is somewhat narrower in *S. pectinata* than *S. bifurcata* (Velichkin, 1979). The molecular and morphological data are consistent with the reduction of *S. pectinata* to synonymy of the earlier-published *S. bifurcata*.

With respect to the North American taxa, three species were monophyletic based on ITS data: *Smelowskia americana* (supported by a 96% bootstrap value), *S. johnsonii* (70% bootstrap value), and *S. pyriformis* (4 accessions with identical sequences). *Smelowskia porsildii*, which is both North American and Asian, also formed a single clade (70% bootstrap value). The other North American taxa, *S. borealis* and *S. media*, were not monophyletic based on ITS data, while relationships of the samples of *S. ovalis* were not resolved by the ITS data.

←

Figure 3. Strict consensus tree of 20 most parsimonious trees generated from analysis of the *trn*L intron sequences. Tree length = 76 (excluding parsimony uninformative characters), CI = 0.88, RI = 0.96. Bootstrap values from 500 replicates (400 trees per rep) appear above branches with > 50% bootstrap support. Accession number as listed in Table 3 is given in parentheses after the species name; all conspecific samples listed within parentheses had identical sequences. The four major clades (*Smelowskia* s.l., *Polyctenium*, Holmgrenii, *Descurainia*) recognized in the analysis and the outgroup taxa are indicated to the right. Asian (A) versus North American (NA) distributions are indicated in bold for species in the ingroup.

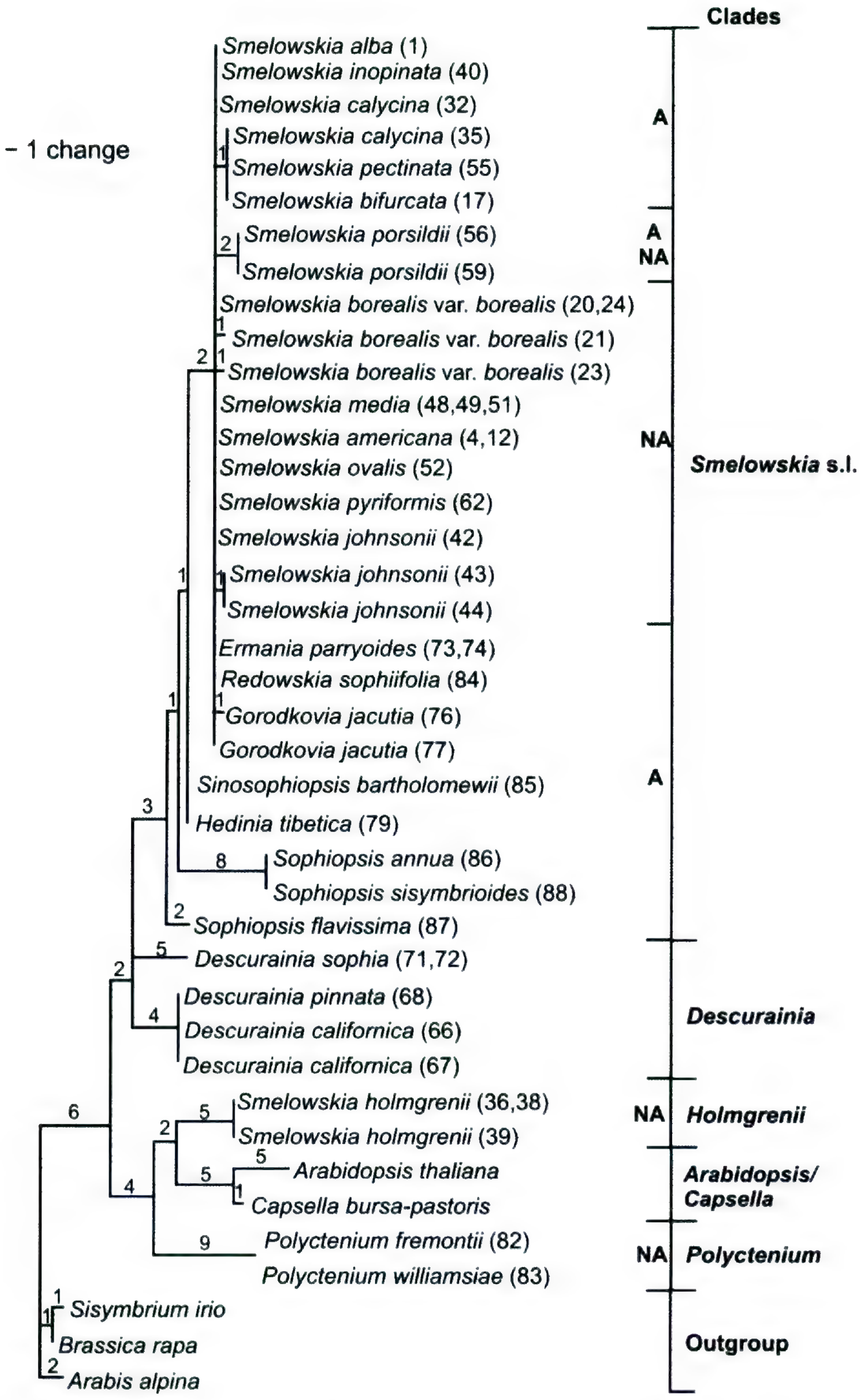


Figure 4. One of the most parsimonious trees based on *trn*L sequence analysis. Tree length = 76 (excluding parsimony uninformative characters), CI = 0.88, RI = 0.96. The number of characters supporting each clade is indicated. The four major clades (*Smelowskia* s.l., *Polyctenium*, Holmgrenii, *Descurainia*) recognized in the analysis and the outgroup taxa are indicated to the right. Asian (A) versus North American (NA) distributions are indicated in bold for species in the ingroup.

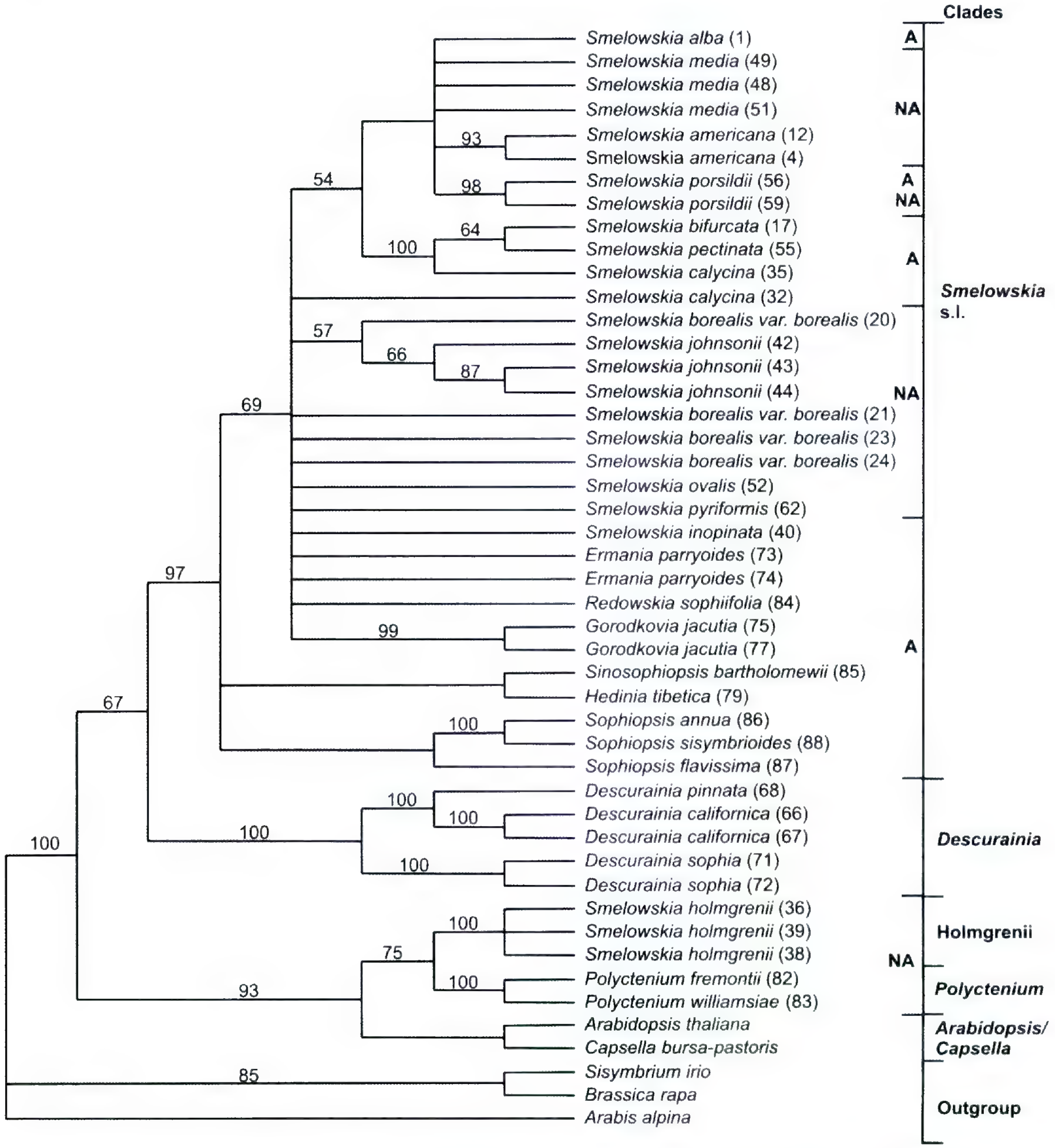


Figure 5. Strict consensus tree of 896 most parsimonious trees generated from analysis of the combined ITS and *trn*L intron sequences. Tree length = 461 (excluding parsimony uninformative characters), CI = 0.60, RI = 0.81. Bootstrap values from 500 replicates (400 trees per rep) appear above branches with > 50% bootstrap support. Accession number as listed in Table 3 is given in parentheses after the species name. The four major clades (*Smelowskia* s.l., *Polyctenium*, Holmgrenii, *Descurainia*) recognized in the analysis and the outgroup taxa are indicated to the right. Asian (A) versus North American (NA) distributions are indicated in bold for species in the ingroup.

Smelowskia ovalis is morphologically a well-defined species easily separated from the other species of the genus by having persistent sepals and ovoid fruits with a distinct style. The accessions corresponding to variety *ovalis* (acc. 52 and 53) had similar ITS sequences, separated by only three steps, whereas variety *congesta* (acc. 54) was more distinct and separated by seven steps from the other two accessions, resulting in a sequence divergence of 1.34%, ca. 10-fold greater than that observed between accessions of other *Smelowskia* taxa. Drury and Rollins (1952) and Rollins (1993) recognized variety *congesta* on the basis of inflorescence shape (i.e., densely congested vs. more lax), silique length (3–6 vs. 2–4 mm long), and trichome type (short and branched vs. long and simple). In contrast to

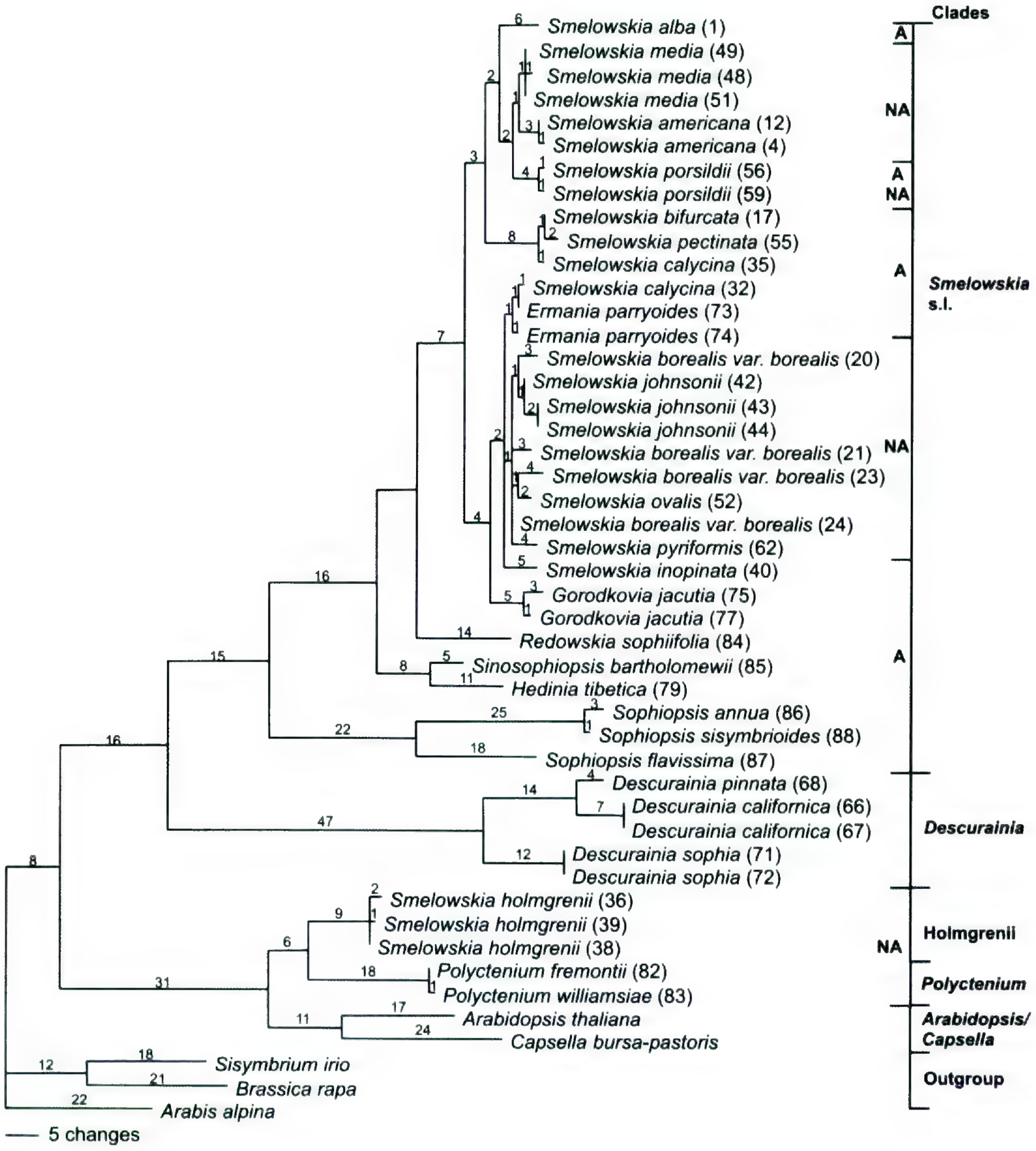


Figure 6. One of the most parsimonious trees based on combined ITS and *trn*L sequence analysis. Tree length = 461 (excluding parsimony uninformative characters), CI = 0.60, RI = 0.81. The number of characters supporting each clade is indicated. The four major clades (*Smelowskia* s.l., *Polyctenium*, Holmgrenii, *Descurainia*) recognized in the analysis and the outgroup taxa are indicated to the right. Asian (A) versus North American (NA) distributions are indicated in bold for species in the ingroup.

the ITS data, which supports the recognition of the two varieties, a critical re-examination of the type material does not support these differences and, therefore, we have proposed the reduction of this variety to synonymy of *S. ovalis* (Table 2).

Based on ITS data, *Smelowskia borealis* was separated into six clades (Fig. 2). The first contained *S. borealis* (acc. 27, 28, and 29), all corresponding to variety *koliana* (Gombócz) W. H. Drury & Rollins and *S. media* (all accessions). The remaining *S. borealis* accessions (var. *borealis*) formed loosely supported clades, except for the clade containing accessions 18, 20, and 22, which was supported by a 94% bootstrap value. *Smelowskia borealis* is highly variable, and some of the varieties (i.e., var. *jordalii*) recognized by Drury and Rollins (1952) merit independent status (see *S. johnsonii* below). Both *S. borealis* and *S. media* are diploid (Table 4), but

Table 4. Chromosome numbers for *Smelowskia*, *Ermania*, *Gorodkovia*, and *Redowskia* taxa reported in the literature.

Taxon	2*n*	Country of origin	Reference
Smelowskia alba	12	Russia	Zhukova & Petrovsky (1980)
S. alba	12	Russia	Zhukova & Petrovsky (1984)
S. alba	12	Russia	Yurtsev & Zhukova (1972)
S. americana	22	Canada (AB)	Packer (1968)
S. americana	12	U.S.A. (CO, UT, WY)	Drury & Rollins (1952)
S. bifurcata	12	Russia	Krogulevich (1976)
S. borealis var. *borealis*[1]	12	U.S.A. (AK)	Murray & Kelso (1997)
S. borealis var. *jordalii*	12	U.S.A. (AK)	Dawe & Murray (1979)
S. borealis var. *koliana*	12	U.S.A. (AK)	Dawe & Murray (1981a)
S. borealis var. *villosa*	12	U.S.A. (AK)	Drury & Rollins (1952)
S. calycina var. *calycina*[2]	12	Russia	Yurtsev & Zhukova (1972)
			Zakharyeva & Astanova (1968)
S. calycina var. *integrifolia*	22	U.S.A. (AK)	Johnson & Packer (1968)
S. calycina var. *integrifolia*	12	U.S.A. (AK)	Murray & Kelso (1997)
S. media[4]	12	U.S.A. (AK)	Dawe & Murray (1981b)
S. porsildii[3]	22	U.S.A. (AK)	Dawe & Murray (1979)
S. porsildii	22	U.S.A. (AK)	Rollins (1993)
S. porsildii	32	Russia	Zhukova & Petrovsky (1984)
S. porsildii	18	Russia	Zhukova & Petrovsky (1984)
S. porsildii	24	Russia	Yurtsev & Zhukova (1972)
			Yurtsev et al. (1975)
S. pyriformis	12	U.S.A. (AK)	Murray & Kelso (1997)
Ermania parryoides	12, 24	Russia	Yurtsev & Zhukova (1972)
			Zhukova & Petrovsky (1984)
E. parryoides	12	Russia	Zhukova (1980)
			Berkutendo et al. (1984)
E. parryoides	24	Russia	Zhukova & Petrovsky (1977, 1980)
Gorodkovia jacutica	12	Russia	Yurtsev & Zhukova (1972)
G. jacutica	36	Russia	Yurtsev & Zhukova (1982)
Redowskia sophiifolia	20	Russia	Yurtsev & Zhukova (1982)

[1] Reported as *S. borealis*.
[2] Reported as *S. calycina*.
[3] Reported as *S. calycina* subsp. *integrifolia* var. *porsildii* (Drury & Rollins) Hultén.
[4] Reported as *S. calycina* subsp. *media* Drury & Rollins.

they differ significantly in the morphology of their caudices, flowers, and fruits. *Smelowskia borealis* has simple and stout caudices, often branched flowering stems, often purple sepals and/or petals, and angustiseptate fruits. By contrast, *S. media* has branched and slender caudices, simple flowering stems, white or cream flowers, and terete or angled fruits. Variety *koliana*, on the other hand, is quite different in fruit morphology (oblong to spatulate vs. obovate) and length (7–18 vs. 3–7(–8) mm long) from variety *borealis*, and it may well deserve to be recognized as a distinct species. Critical morphological, cytological, and molecular studies are needed to understand the phylogenetic relationships within the *S. borealis* and *S. media* complexes.

Smelowskia johnsonii, recently described by Mulligan (2001), would appear to be the same taxon as *S. borealis* var. *jordalii* W. H. Drury & Rollins. We have not examined the type of the latter taxon, but the original description is similar to the type collection of *S. johnsonii*, except the latter has shorter fruits that are not spatulate. *Smelowskia johnsonii* is morphologically very distinct from all of the North American species and is easily distinguished by its densely white villous leaves, minute styles (usually less than 0.5 mm long), caducous calyx, and ellipsoid, slightly angustiseptate fruits.

The molecular data support the recognition of the varieties of *Smelowskia calycina* (Drury & Rollins, 1952; Rollins, 1993, Table 2) as separate species as in Velichkin (1979), with *S. americana*, *S. calycina*, *S. media*, and *S. porsildii* each forming distinct clades. *Smelowskia calycina* is strictly an Asian taxon, and based on ITS data (Fig. 2) was divided into two clades (acc. 30, 31, 34, 35 and 32, 33). However, no obvious morphological differences were apparent between the herbarium spec-

imens in each clade. The ITS data for accession 35 support the inclusion of *S. koelzii* in *S. calycina* by Botschantzev (1968) and Czerepanov (1995). The North American *S. media* and *S. porsildii* are distinct cytologically (the former is diploid and the latter is polyploid with various numbers; see Table 4). They also differ in their leaves and fruits. In *S. media* the cauline leaves are divided and the fruits are widest above the middle, whereas in *S. porsildii* the cauline leaves are undivided and the fruits are widest at the middle. The remaining North American varieties of *S. calycina* (var. *americana* (Regel & Herder) W. H. Drury & Rollins and var. *integrifolia* (Seeman) Rollins), as treated by Drury and Rollins (1952), Rollins (1993), and Mulligan (2001), should be recognized as *S. americana*, the oldest name available at the specific rank. Velichkin (1974, 1979) recognized four distinct North American species (*S. americana*, *S. lineariloba*, *S. lobata*, and *S. spathulatifolia*; see Table 2) in what is treated here as *S. americana*. However, Velichkin's delimitation of the last species included material that belongs to *S. porsildii*. Further studies are needed to elucidate whether or not *S. spathulatifolia* merits recognition.

2. *SMELOWSKIA* S.L. CLADE

Representatives of *Ermania*, *Gorodkovia*, *Hedinia*, *Redowskia*, *Sinosophiopsis*, and *Sophiopsis* were included within a well-supported clade along with *Smelowskia* s. str., with bootstrap values of 90 and 91% based on ITS and *trn*L sequence data, respectively. Except for the three *Sophiopsis* species, the degree of sequence divergence from *Smelowskia* taxa for the other five genera fell within the range observed among *Smelowskia* s. str. Each will be discussed separately below based on ITS and *trn*L divergence from *Smelowskia* s. str.

Ermania *Cham. ex. Botsch.*

The ITS data fully supported the earlier taxonomic transfer by Drury and Rollins (1952) of *Ermania borealis* to *Smelowskia*. These authors further indicated (1952: 88) that "the type species of *Ermania*, *E. parryoides*, might with some propriety also be included in *Smelowskia*." Although Polunin (1959) transferred *E. parryoides* to *Smelowskia*, *Ermania* has been retained by most authors as a separate genus on the basis of having elongated latiseptate siliques, i.e., strongly flattened parallel to the septum. In the analysis of ITS sequence data, *E. parryoides* formed a sister group to two accessions of *Smelowskia calycina* in 78% of the maximally parsimonious trees (MPT) with a sequence divergence of only 0.17–0.67%. Sequence divergence from other *Smelowskia* taxa was also less than 2.71%, supporting the taxonomic inclusion of *E. parryoides* in *Smelowskia*. Data for the *trn*L intron provided similar evidence for its inclusion in *Smelowskia*, based on sequence divergence of 0–1.01%. With the exception of accumbent versus incumbent cotyledons, all its morphological features can be accommodated in the current circumscription of *Smelowskia* (Table 1). *Ermania parryoides* is reported to have chromosome numbers of $2n = 12$, 24, as in other species of *Smelowskia* (Table 4). Therefore, the morphological, cytological, and molecular data clearly support Polunin's (1959) transfer of *E. parryoides* to *Smelowskia*.

Gorodkovia *Botsch. & Karav.*

Both ITS and *trn*L sequence data indicate the closeness of *Gorodkovia* to *Smelowskia* s. str. Based on ITS data, sequence divergence between *Gorodkovia* and Asian *Smelowskia* taxa ranged from 1.51% to 3.40% and were only 0–1.22% based on *trn*L data. This monotypic genus, described in Botschantzev and Karavaev (1959), is distributed in eastern Siberia and the Russian Far East (Czerepanov, 1995). With the exception of having biseriate instead of uniseriate seed arrangement, all other morphological features of *G. jacutica* fall within the current delimitation of *Smelowskia* (Table 1). Similar to the Old World *Smelowskia* taxa, it has a chromosome number of $2n = 12$, 36. Morphological, cytological, and molecular data do not support the maintenance of *Gorodkovia* as a genus distinct from *Smelowskia*.

Redowskia *Cham. & Schltdl.*

Both ITS and *trn*L sequence data indicate the closeness of the monotypic genus *Redowskia* to *Smelowskia* s. str. Based on ITS sequence data, *R. sophiifolia* was separated from the Asian taxa of *Smelowskia* by a sequence divergence of only 2.02–3.76% and 0–1.01% based on *trn*L data. This monotypic genus occurs in eastern Siberia (Czerepanov, 1995). Schulz (1924, 1936) placed *Redowskia* and *Smelowskia* in subtribe Descurainiinae. *Redowskia* differs from *Smelowskia* in fruit shape, slightly 2-lobed versus entire stigmas, and biseriate versus uniseriate seed arrangement (Table 1). It also appears to have a distinct chromosome number of $2n = 20$, as compared to $2n = 12$, 18, 22, 24, and 32 in species of *Smelowskia* (Table 4). Despite these morphological and cytological differences, ITS and *trn*L sequence data do not provide suffi-

cient support for the maintenance of *Redowskia* as distinct from *Smelowskia*.

Hedinia *Ostenf.*

Both ITS and *trn*L sequence data indicate the closeness of *Hedinia tibetica* to *Smelowskia* s. str. On the basis of ITS sequence data, *Hedinia tibetica* is separated from the Asian *Smelowskia* (*S. alba, S. calycina*) by a sequence divergence of only 2.72–3.95%. *Hedinia*, a central Asian genus (Table 1), contains four species, including one of *Hediniopsis* Botsch. & Petrovsky recently reduced to synonymy of *Hedinia* (Appel & Al-Shehbaz, 2002). *Hedinia tibetica* was originally described under the illegitimate name *Hutchinsia* (Thomson, 1852) and was later transferred by Lipsky (1904) to *Smelowskia*. Velichkin (1979) indicated that *Smelowskia* and *Hedinia* are closely related. Except for having bracteate instead of ebracteate racemes and lacking the median nectar glands, there are no other characters that clearly separate the two genera (Table 1). In fact, as delimited by Czerepanov (1995), *Hedinia* has species with bracteate and ebracteate racemes. These two character differences are unreliable for the separation of these two genera, as for most other genera of the family (Al-Shehbaz, 2000, 2001). Morphological and molecular data support Lipsky's transfer of *H. tibetica*, the generic type, to *Smelowskia*. Comparative morphological and molecular studies are required for *H. altaica* Pobed., *H. czukotica* (Botsch. & V. V. Petrovsky) Jurtzev, Korobkov & Balandin, and *H. mongolica* (Kom.) Velichkin.

Sinosophiopsis *Al-Shehbaz*

Within the *Smelowskia* s.l clade from the ITS analysis (Figs. 1, 2), *Sinosophiopsis bartholomewii* was the sister taxon to *Hedinia tibetica*, forming a loosely supported clade (65% bootstrap value). It was separated from Asian *Smelowskia* taxa by ca. 13 steps and a sequence divergence of 2.54–3.77%. Based on *trn*L data, it is separated by only two steps and a sequence divergence of 0.82–1.85%. It is one of three species recently described in this Chinese genus (Al-Shehbaz, 2000, 2002). *Sinosophiopsis* differs from *Smelowskia* by the annual growth habit and obscure midvein on the fruit valves and differs from *Hedinia* in an even greater number of morphological features (Table 1). Further molecular studies on *Sinosophiopsis furcata* Al-Shehbaz and *S. heishuiensis* (W. T. Wang) Al-Shehbaz, are needed to determine the distinctness of *Sinosophiopsis* from *Hedinia* and *Smelowskia*.

Sophiopsis *O. E. Schulz*

Although included within the *Smelowskia* s.l. clade, the three *Sophiopsis* taxa showed the greatest divergence from *Smelowskia* s. str., with a sequence divergence of 4.65–6.45%. Based on both ITS and *trn*L sequence data, this central Asian genus of four species (Schulz, 1924; Botschantzev, 1952), three of which are included in this paper, was not monophyletic. *Sophiopsis annua* and *S. sisymbrioides* formed a well-supported clade with a bootstrap value of 100% and sequence divergence of only 0.67% between them, whereas *S. flavissima* was separated by 35 steps and sequence divergence of 7.42% from the latter two species based on ITS data and by 11 steps and sequence divergence of 3.33% based on *trn*L data. *Sophiopsis flavissima* differs from the other species of *Sophiopsis* by having stems with long, simple or forked trichomes instead of dendritic ones, and perhaps merits independent generic status. Schulz (1924, 1936) placed *Sophiopsis* and *Smelowskia* in the subtribe Descurainiinae, and Velichkin (1979) indicated that *Smelowskia* was closely related to *Sophiopsis*. Morphological differences between the two genera are limited (Table 1). Schulz (1924, 1936) separated *Sophiopsis* from *Smelowskia* solely on the basis of seeds that become mucilaginous versus non-mucilaginous, respectively, when wetted, a variable character in many genera of Brassicaceae. Both molecular data sets support the inclusion of *Sophiopis* in the *Smelowskia* s.l. clade. However, the genus is not monophyletic and is the most distant in the clade. Further study of the group, including the fourth species, *S. micrantha* Botsch. & Vved., is required in order to resolve its closest relatives and lack of monophyly.

3. *POLYCTENIUM* GREENE AND *SMELOWSKIA HOLMGRENII*

The ITS sequence data indicate that the North American *Polyctenium* (*Polyctenium* clade) as delimited by Rollins (1938, 1993), is monophyletic and, together with *Smelowskia holmgrenii* (Holmgrenii clade), forms a well-supported clade (93% bootstrap value) that is separated by 32 steps from the *Smelowskia* s.l. clade. *Arabidopsis thaliana* and *Capsella bursa-pastoris*, initially included in the phylogenetic analysis as outgroup species, were sister species to the Holmgrenii and *Polyctenium* clades in a clade supported by a 91% bootstrap value. Similarly for the *trn*L data, *Polyctenium* spp. and *S. holmgrenii* were included in the same clade (63% bootstrap value), along with *A. thaliana* and *C. bursa-pastoris* and separated from the *Smelows-*

kia s.l. clade by nine steps. Although *A. thaliana* and *C. bursa-pastoris* are members of different tribes, several molecular studies (Galloway et al., 1998; Koch et al., 2001) suggest these two taxa to be more closely related than previously thought. The unexpected position of these two genera in our phylogenetic tree within the ingroup as sister to *S. holmgrenii* and *Polyctenium* (subtribe Descurainiinae, tribe Sisymbrieae) underlines the profound problems in tribal classification of the Brassicaceae. However, this is outside the scope of the current study. Comprehensive molecular studies along with critical re-evaluation of morphological characters are needed to obtain a robust phylogenetic framework that reflects a more natural classification system.

Rollins (1938) separated *Smelowskia* from *Polyctenium* by the petiolate, pliable leaves covered with dense whitish tomentum, caudices covered by leaf bases, petals differentiated into blade and claw, and 2 to 10 ovules per ovary. *Polyctenium* was said to have non-petiolate, wiry leaves, sparse, never whitish pubescence, caudices free of leaf bases, petals tapering from apex to base, and 12 to 28 ovules per ovary. In his original description of *S. holmgrenii*, Rollins (1950) expressed the difficulty in assigning this species to a genus. He placed it in *Smelowskia* based on fruit morphology (terete, few-seeded). He also indicated that it differed from the other two North American *Smelowskia*, *S. calycina* and *S. ovalis*, by lacking the white dense tomentum and by having entire, stiff, basal leaves. In addition to their rigid, leathery leaves and almost exclusively simple and forked rigid trichomes, *Polyctenium* species and *S. holmgrenii* also differ from *Smelowskia* s.l. by having an obscure instead of prominent midvein (Table 1). *Smelowskia* is essentially an arctic-alpine genus with two areas of concentration, the Cascade and Rocky Mountains of western North America and mountainous areas of central and eastern Asia; *Polyctenium* inhabits semiarid areas at relatively low elevation in Nevada and adjacent California, southeastern Oregon, and southern Idaho, whereas *S. holmgrenii* is a narrow endemic at middle elevations in Nevada (Rollins, 1950, 1993). Velichkin (1979) indicated that *Smelowskia*, including *S. holmgrenii*, was closely related to *Polyctenium* and *Capsella*, and the molecular data herein do not contradict the association of these genera. Morphological, geographical, and both sets of molecular data, therefore, suggest evidence that *S. holmgrenii* is more closely related to *Polyctenium* than to *Smelowskia*. The ITS and combined ITS/*trn*L data were consistent with the inclusion of *S. holmgrenii* in *Polyctenium*; however, the *trn*L sequence data provided limited support (bootstrap value < 50%) for their placement in a single clade, as shown in Figure 4. The inclusion of *Arabidopsis* and *Capsella* in the same clade with these taxa (Figs. 1, 2, 4–6), supports the treatment of *S. holmgrenii* as a separate genus until further studies are completed for this group of related taxa.

4. *DESCURAINIA* WEBB & BERTHEL.

Based on ITS sequence data, *Descurainia* formed a well-supported clade (100% bootstrap value) that was very distinct from *Smelowskia*, separated by 45 steps from both the *Smelowkia* s.l. clade and the *Polyctenium* clade (Figs. 1, 2). *Descurainia* was divided into two distinct clades for both ITS and *trn*L data. The difference between the two clades was particularly apparent for the *trn*L intron with *D. californica* and *D. pinnata* having two unique indels, including a 5 bp (114–118 bp) and a 60 bp deletion (229–288 bp) compared to *D. sophia*. *Descurainia*, a genus of about 40 species, is native to many temperate parts of the world, with important areas of diversity in both North and South America (Rollins, 1993). It is clearly distinct from the rest of the genera included in the ingroup. Morphologically, *Descurainia* is also very distinct from *Smelowskia* by having glandular papillae, exclusively dendritic trichomes, mostly yellow flowers, and valves without a keel (Table 1). Schulz (1924, 1936) placed both genera in the subtribe Descurainiinae, and the molecular data suggest that *Descurainia* is very distantly related to the *Smelowskia* s.l. clade. Molecular data also indicate that *D. sophia*, the generic type, is distinct from the other two species, and further phylogenetic studies are needed on the genus.

In summary, both the ITS and *trn*L data indicated low levels of genetic differentiation among species of *Smelowskia* s. str. (excluding *S. holmgrenii*), in contrast to a wide geographic distribution (Velichkin, 1979: map 169) covering central and northern Asia and western North America. The molecular-based *Smelowskia* s.l. clade also contained Asian taxa, *Ermania*, *Gorodkovia*, *Hedinia*, *Redowskia*, *Sinosophiopsis*, and *Sophiopsis*, and thus supports central Asia as the center of origin of *Smelowskia* s. str., followed by diversification in Asia and North America, subsequent to migration into arctic-alpine regions of western North America via the former Bering land bridge as was suggested by Rollins (1982). Such patterns were also suggested for various disjunct Brassicaceae genera, among them *Stroganowia* (K. Mummenhoff, unpublished data) and *Lepidium* (Mummenhoff et al., 2001b).

ITS sequence divergence estimates, i.e., corrected pair-wise distance values based on Kimura-2-parameter model, ranged from 0 to 4.1% within *Smelowskia* s. str., and up to 6.45% within the *Smelowskia* s.l. clade; whereas *trn*L sequence divergence estimates ranged from 0 to 1.85% within *Smelowskia* s. str., and up to 3.71% within the *Smelowskia* s.l. clade. Recent calculations for several Brassicaceae show that corrected ITS distance values (Kimura-2-parameter model) of 1% correspond to ~ 0.5 to 1 million years (Koch & Al-Shehbaz, 2002, 2004), indicating pleistocenic speciation within *Smelowskia* as a whole. Similar rapid radiation and migration from Asia to Europe during the Pleistocene was observed in *Noccaea* (Koch & Al-Shehbaz, 2004) and *Draba* (Koch & Al-Shehbaz, in prep.) and from Central Europe to Scandinavia and the arctic region in *Cochlearia* (Koch et al., 1998, 1999b).

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PHYLOGENETIC RELATIONSHIPS OF *VULPIA* AND RELATED GENERA (POEAE, POACEAE) BASED ON ANALYSIS OF ITS AND *trn*L-F SEQUENCES[1]

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Abstract

A phylogenetic study of *Vulpia*, fine-leaved *Festuca* (*Festuca* subg. *Festuca* p.p.), and other related genera of the tribe Poeae (Poaceae) has been conducted using both separate and combined analyses of DNA sequences from the nuclear ITS region and the chloroplast *trn*L-F region. All five sections of *Vulpia* (sects. *Vulpia, Monachne, Spirachne, Loretia, Apalochloa*) and three sections and one subsection of fine-leaved *Festuca* (sects. *Eskia, Festuca, Aulaxyper,* subsect. *Exaratae*) were included in the analysis. Six minor annual genera that have been considered in the past to be related either to *Vulpia* or to these fescues (*Psilurus, Ctenopsis, Cutandia, Narduroides, Micropyrum, Wangenheimia*) were also analyzed in order to estimate an evolutionary framework for this poorly known group of ephemeral or thin-leaved grasses. Single representatives of other less related groups of Poeae (*Festuca* subg. *Schedonorus* and *Drymanthele, Lolium, Dactylis, Poa, Puccinellia, Sesleria*), Triticeae (*Secale*), and Brachypodieae (*Brachypodium*) were also studied. Phylogenetic analyses were performed based on parsimony and Bayesian inference criteria using *Brachypodium distachyon* as outgroup. Our results indicate that *Vulpia* and the fine-leaved *Festuca* are, respectively, polyphyletic and paraphyletic assemblages of several taxa. A well-supported monophyletic group that encompasses the fine-leaved *Festuca* and *Vulpia* lineages as well as the other six ephemeral genera (FEVRE) has been obtained from both the separate and the combined ITS and *trn*L-F analyses. Within this FEVRE clade *Festuca* sect. *Eskia* is shown to be a paraphyletic assemblage basal to the other taxa; the core of the FEVRE clade contains four supported clades representing, respectively, the lineages Aulaxyper + Vulpia pro parte (diploid), Festuca + Wangenheimia, Psilurus + Vulpia pro parte (polyploid), and Spirachne + Monachne + Loretia. *Vulpia unilateralis* (Apalochloa) constitutes a monospecific lineage with apparent but unsupported affinities to some of its potential closer relatives. Representatives of all the *Vulpia* sections except those belonging to typical section *Vulpia* join in a paraphyletic poorly supported assemblage that also includes *Cutandia, Festuca plicata,* and *Ctenopsis.* Two of the studied annual genera, *Micropyrum* and *Narduroides,* show distant evolutionary placements in the ITS and *trn*L-F trees. The *Festuca* subsect. *Exaratae* taxa belong to a phylogenetic lineage diverging from those of the *Festuca ovina* (sect. *Festuca*) and *F. rubra* (sect. *Aulaxyper*) fescues. Nucleotide substitution rates show significant differences between most perennial and annual lineages; stabilized selection is maintained in the slowly diverging perennial groups, whereas the rapid adaptive evolutionary processes shown by the annual taxa may have resulted in an increased rate in cladogenesis. The Mediterranean region is hypothesized as the likely place of divergence of these grass lineages.

Key words: *Ctenopsis, Cutandia, Festuca,* FEVRE group, ITS, *Micropyrum, Narduroides,* phylogeny, *Psilurus,* relative rate test, *trn*L-F, *Vulpia, Wangenheimia.*

The genus *Vulpia* and other related genera of ephemeral grasses, mostly native to the Mediterranean region, have never been investigated from a modern phylogenetic perspective. Single representatives of *Vulpia* have been included, however, in three recent phylogenetic studies of *Festuca,* a large

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genus of perennial species that contains important forage grasses distributed on all five continents. The pioneer work of Darbyshire and Warwick (1992), based on analysis of chloroplast restriction sites, first established the evolutionary links between *Vulpia* (*V. myuros*) and *Festuca* subg. *Festuca*. Subsequent studies by Charmet et al. (1997) and Torrecilla and Catalán (2002), based on analyses of ribosomal DNA sequences, also confirmed the close relationships between *Vulpia* (*V. myuros* and *V. fasciculata*) and the fine-leaved fescues, which include *Festuca* sects. *Festuca*, *Aulaxyper*, and *Eskia*. These three mentioned works have demonstrated that *Festuca* is a paraphyletic complex and that *Vulpia* and *Lolium* fall within different *Festuca* clades. However, whereas the phylogenetic proximity of *Lolium* and *Festuca* subg. *Schedonorus* (*Schedonorus*) has been analyzed in depth (Charmet et al., 1997; Gaut et al., 2000), very little information has been obtained with respect to the relationships between *Vulpia* and *Festuca* subg. *Festuca*.

Broad sampling of *Festuca* representatives was included in the study by Torrecilla and Catalán (2002) in which up to ten different lineages of the genus *Festuca* were incorporated into the analysis. These authors demonstrated that "*Festuca* s.l." (including *Vulpia* and *Lolium*) is monophyletic, yet split into two diverging groups, the so-called "broad-leaved" *Festuca* and the "fine-leaved" *Festuca*. Within this first group *Lolium* and *Schedonorus* formed a well-supported clade, whereas in the second one *Vulpia* (*V. fasciculata*) was associated with *Festuca* sect. *Aulaxyper*.

The taxonomic treatments of *Vulpia*, the fine-leaved *Festuca*, and the six related annual genera have varied over the last two centuries (Table 1). *Vulpia* has been considered as a part of the genus *Festuca* by some authors or as an independent genus by others. Linnaeus (1753) first described two of the present species of *Vulpia* under *Festuca*, including the type, *Vulpia* [= *Festuca*] *myuros*, and *Vulpia* [= *Festuca*] *bromoides*. Gmelin (1805) separated *Vulpia* from *Festuca* based on its annual habit, long-awned lemma, and very unequal glumes. Hackel (1887) subordinated *Vulpia* as a subgenus of *Festuca*. Although some later authors still maintained *Vulpia* within *Festuca*, most contemporary agrostologists have considered *Vulpia* as a genus on its own (Stace & Cotton, 1980; Clayton & Renvoize, 1986). The circumscription of the genus *Vulpia* has changed depending on the inclusion or exclusion of different genera, subgenera, or sections within it (summarized in Stace, 1981). The *Vulpia* species differ in their breeding system, number and size of anthers, spikelet structure, number of fertile/unfertile florets, and shape and size of the lemma callus (Cotton & Stace, 1977; Stace, 1978a). *Vulpia* sect. *Loretia* has been considered the most similar group to *Festuca* as it includes robust annuals as well as the three known perennial species of *Vulpia* and shows strong chasmogamy syndromes (Cotton & Stace, 1977). *Vulpia* sects. *Monachne* and *Spirachne* show intermediate traits between *Vulpia* sects. *Loretia* and *Vulpia* trending toward reduction in size and increasing self-fertility; these groups encompass both chasmogamous and cleistogamous species, with sterile distal florets and shorter anthers in the proximal fertile ones. *Vulpia* sect. *Vulpia* has been interpreted as the most advanced group, as the majority of its taxa are strongly cleistogamous species with single and small-anthered fertile florets. Section *Apalochloa* is a quite distinct taxon; its only species (*Vulpia unilateralis*) also shows a reduced habit and reproductive organs, but its flowers are chasmogamous. *Apalochloa* has been treated as an independent genus (= *Nardurus* (Bluff, Nees & Schauer) Rchb.) by several authors (summarized in Stace, 1978a); however, as most of its features are similar to *Vulpia* it has been classified within it (Stace, 1978a; Stace, 1981 amended). Cotton and Stace (1976) found the chromosome number to be fixed within each *Vulpia* species (Table 1) and to show a geographical distribution pattern.

"*Festuca* sensu stricto" (subg. *Festuca* p.p.), as circumscribed by Torrecilla and Catalán (2002), includes at least four distinct groups (as sects. *Festuca*, *Aulaxyper*, *Eskia*, and subsect. *Exaratae*), though their evolutionary relationships have not been conclusively established yet. These taxa are characterized by their perennial habit and short-awned lemma, traits in contrast to *Vulpia*, though neither condition is free from homoplasy (Cotton & Stace, 1977). Other taxa previously included in *Festuca* by Hackel (1882) and Krivotulenko (1960) (sects. *Subbulbosae*, *Scariosae*, and *Pseudoscariosae*) do not belong to this group as they are members of the "broad-leaved" *Festuca* clade (Torrecilla & Catalán, 2002).

Festuca sect. *Festuca* includes the type species *F. ovina* (within a "*Festuca ovina*" complex), whereas section *Aulaxyper* encompasses the red fescues ("*Festuca rubra*" complex). Hackel (1882) classified these groups under one section *Ovinae* [= *Festuca*] though separated into two different series by the possession of exclusively intravaginal shoots (sect. *Festuca*) versus extravaginal and intravaginal ones (sect. *Aulaxyper*). Together sections *Festuca* and *Aulaxyper* account for most species described

Table 1. Taxonomic treatments adopted by different authors for the fine-leaved *Festuca*, *Vulpia*, and other related genera.

Hackel (1882), Hackel (1887)	St-Yves (1922)	Cotton & Stace (1977), Stace (1981)	Clayton & Renvoize (1986)	Torrecilla & Catalán (2002)	This study	No. of taxa[1]	Ploidy[2]
Festuca	*Festuca*		*Festuca*	*Festuca*	*Festuca*		
subg. *Festuca*			subg. *Festuca*	subg. *Festuca*			
sect. *Ovina*	sect. *Ovinae*						
	subsect. *Legitimae*			sect. *Festuca*	sect. *Festuca*		
ser. *Intravaginales*	ser. *Intravaginales*			subsect. *Festuca*	subsect. *Festuca*	>90	2*x*, 4*x*, 6*x*, 8*x*, 10*x*, 12*x*
ser. *Extravaginales* vel *Mixtae*	ser. *Extravaginales* vel *Mixtae*			sect. *Aulaxyper*	sect. *Aulaxyper*	>20	2*x*, 4*x*, 6*x*, 8*x*, 10*x*
	subsect. *Exaratae*			sect. *Festuca*	sect. *Festuca*		
	ser. *Intravaginales*			subsect. *Exaratae*	subsect. *Exaratae*	ca. 13	2*x*, 4*x*
	ser. *Extravaginales* vel *Mixtae*						
sect. *Variae*	sect. *Variae*			sect. *Eskia*	sect. *Eskia*	ca. 24	2*x*, 4*x*
ser. *Intravaginales*	ser. *Intravaginales*						
Festuca				sect. *Pseudatropis*	sect. *Pseudatropis*	1	2*x*, 4*x*
subg. *Vulpia*	*Vulpia*	*Vulpia*	*Vulpia*	*Vulpia*	*Vulpia*		
	sect. *Vulpia*	sect. *Vulpia*			sect. *Vulpia*	ca. 12	2*x*, 4*x*, 6*x*
	sect. *Monachne*	sect. *Monachne*			sect. *Monachne*	3	2*x*
	sect. *Spirachne*	sect. *Spirachne*			sect. *Spirachne*	1	2*x*
	sect. *Loretia*	sect. *Loretia*			sect. *Loretia*	8	2*x*
	sect. *Apalochloa*	sect. *Apalochloa*			sect. *Apalochloa*	1	2*x*
	Ctenopsis	sect. *Ctenopsis*			*Ctenopsis*	4	2*x*
	Cutandia	*Cutandia*			*Cutandia*	6	2*x*
	Micropyrum	*Micropyrum*			*Micropyrum*	3	2*x*
	Narduroides	*Narduroides*			*Narduroides*	1	2*x*
	Psilurus	*Psilurus*			*Psilurus*	1	4*x*
	Wangenheimia	*Wangenheimia*			*Wangenheimia*	2	2*x*

[1] Cotton & Stace (1977); Maire (1955); Markgraf-Dannenbeg (1980); Stace (1978a, 1978b).

[2] Cotton & Stace (1976); Ainscough et al. (1986); Kerguélen & Plonka (1989); Fuente et al. (2001); Torrecilla & Catalán (2002) (common ploidy levels are underlined).

in the genus, which are widespread in the Northern Hemisphere. Section *Festuca* presents ploidy levels from diploids to duodecaploids, though the high polyploids are uncommon, most taxa having $2n = 2x$ and $4x$–$6x$; conversely, section *Aulaxyper*, though showing a similar diversity, is richer in taxa with $2n = 6x$ and $8x$ ($10x$), and tetraploids and diploids are very rare (Ainscough et al., 1986).

Exaratae was described by Saint-Yves (1922) as a subsection of section *Ovinae* (= *Festuca*) based on the strongly invaginated leaf-sheaths shown by these plants (Saint-Yves, 1913). This Hackelian character was used by Saint-Yves (1922) to separate his subsection *Exaratae* from his typical subsection *Legitimae* in *Festuca* (= sects. *Festuca* and *Aulaxyper*; cf. Torrecilla & Catalán, 2002). The *Exaratae* group fescues are mostly local endemics from the Mediterranean basin and surrounding mountains, with ploidy levels $2n = 2x$ and $4x$.

Several annual genera of Poeae have been grouped in a *Vulpia–Desmazeria* complex: *Vulpia*, *Ctenopsis*, *Wangenheimia*, *Micropyrum*, *Castellia*, *Narduroides*, *Loliolum*, *Catapodium*, *Desmazeria*, *Cutandia*, *Vulpiella*, *Sclerochloa* (Stace, 1981). Four (*Ctenopsis*, *Wangenheimia*, *Micropyrum*, and *Castellia*) were characterized as close allies of *Vulpia*, two others (*Narduroides* and *Loliolum*) as intermediate between *Vulpia* and *Desmazeria*, and the remainder as more related to *Desmazeria*. *Desmazeria*, *Catapodium*, and *Cutandia* were recently classified by Soreng and Davis (2000) as belonging to their "Parapholiinae" subtribe, and *Sclerochloa* as a member of their "*Puccinellia* complex," according to their phylogenetic study of Pooideae based on combined analysis of chloroplast restriction sites and structural characters. None of those groups were included in their "Loliinae" clade (= Festucineae C. Presl.; sensu Tzvelev, 1982), where *Festuca* is nested. *Ctenopsis* is similar to *Vulpia* in several floral and leaf-blade traits (Paunero, 1963); it has been treated as a section of the latter (Clayton & Renvoize, 1986) though it differs in inflorescence type and hilum length. *Ctenopsis* has been considered to be close to but separated from *Vulpia* (Cotton & Stace, 1977). *Cutandia* has also been classified as an independent rather different genus from *Vulpia* (Stace, 1978b). *Narduroides*, *Wangenheimia*, and *Micropyrum* were once included in the heterogeneous genus *Nardurus* s.l. (= *Apalochloa* p.p.: Stace, 1978a) based on their annual habit and spicate to racemose inflorescence. However, these three show enough distinct morphological traits to merit generic status (Stace, 1978a). Clayton and Renvoize (1986) even included *Narduroides* in the separate tribe Hainardieae Greuter. The latter authors considered that *Psilurus*, a monotypic isolated Mediterranean genus, was close to *Vulpia*.

Vulpia, *Ctenopsis*, *Micropyrum*, *Narduroides*, and *Cutandia* have been classified as members of the genus *Festuca* by different authors (summarized in Stace, 1981). *Wangenheimia* and *Psilurus* have been considered close to *Vulpia* (Stace, 1981). Likely these predominantly diploid lineages radiated in the Mediterranean area, the region in which they are endemic. A second divergence of polyploid Northern-Hemisphere *Festuca rubra* and *F. ovina* taxa from more ancestral Mediterranean fine-leaved diploids is also considered likely (Kerguélen & Plonka, 1989; Dubcovsky & Martinez, 1992).

In order to test these evolutionary scenarios we studied representatives of the five recognized sections of *Vulpia*, of four sections and subsections of fine-leaved *Festuca*, and of the small genera *Psilurus*, *Ctenopsis*, *Cutandia*, *Narduroides*, *Micropyrum*, and *Wangenheimia* (see Table 2). Phylogenetic reconstructions are based on both independent and simultaneous analyses of DNA sequences from the nuclear ribosomal region (ITS1-5.8S-ITS2) and from the chloroplast *trn*L-F region (*trn*-Leu intron—*trn*-Leu 3′ exon—*trn*L-F spacer). The ITS region has proved useful for resolving the phylogeny of *Festuca* and its allies (Charmet et al., 1997; Gaut et al., 2000; Torrecilla & Catalán, 2002) due to concerted evolution (Baldwin et al., 1995) and a moderate rate of mutation (Torrecilla & Catalán, 2002). The chloroplast *trn*L-F region has demonstrated its phylogenetic value in other Poeae groups (Brysting et al., 2000). The combined analysis of the two different genomic data sources is intended to obtain a consensus phylogeny and to interpret the potential incongruences that might appear in the separate nuclear and chloroplast phylogenetic reconstructions, a subject of importance to resolve the phylogeny of this group of grasses where reticulation has played a major role in speciation.

Rates of evolution differ significantly between lineages of fast-to-slow reproducing plants (Bousquet et al., 1992; Gaut et al., 1992, 1996; Barraclough et al., 1996; Barraclough & Savolainen, 2001). This phenomenon is particularly evident for the grasses, which include some of the most rapidly evolving sequences within the monocotyledons (Gaut et al., 1992). Annual or short-lived perennial grass species that propagate rapidly are expected to show higher genomic variability than their respective long-lived perennial congeners, suggesting a release from stabilized selection (Gaut et al., 1997). Different substitution rates derived from diverse generation times or alternative reproductive strategies could affect the reconstruction of phylo-

Table 2. List of taxa included in the phylogenetic ITS—*trn*L-F study of *Vulpia*, fine-leaved *Festuca*, and related genera with sources and GenBank accession numbers. Order of ingroup taxa follows that indicated in Table 1. Abbreviations: JACA—Herbario del Instituto Pirenaico de Ecología de Jaca; UZ—Herbario de la Universidad de Zaragoza; LEI—Leicester University Herbarium; CAS—Clive Anthony Stace collection; JALR—José Ángel López-Rodriguez collection; PC—Pilar Catalán collection; PT—Pedro Torrecilla collection; SP—Samuel Pyke collection; JM—Jochen Müller collection.

Taxa[1]	Source	Ploidy level[2]	GenBank accession No.	
			ITS	*trn*L-F
Festuca L. (type *F. ovina* L.)				
sect. *Festuca* (type *F. ovina* L.) ("*F. ovina* complex")				
subsect. *Festuca* (type *F. ovina* L.)				
Festuca alpina Suter	Torrecilla & Catalán (2002); Spain: Huesca: Pyrénées: Vallibierna	2*x*[a]	AF303415	AF478522
Festuca aragonensis (Willk.) Fuente & Ortúñez	Spain: Zaragoza: Moncayo JALR 01174 a (UZ)	4*x*[b]	AF519975	AF495884
Festuca clementei Boiss.	Spain: Granada: Sierra Nevada: Veleta PC-JALR-PT 81 (UZ)	2*x*[a]	AF478482	AF478524
Festuca frigida (Hack.) K. Richt.	Spain: Granada: Sierra Nevada: Laguna Aguas Verdes PC-JALR-PT 80 (UZ)	2*x*[b]	AF478481	AF478521
Festuca glacialis Miégev. ex Anon.	Torrecilla & Catalán (2002); Spain: Huesca: Pyrénées: Cotiella	2*x*[a]	AF303428	AF478523
Festuca hystrix Boiss.	Spain: Almería: Sierra de Gádor: Morrón Observatorio PC-JALR-PT 31 (UZ)	2*x*[b]	AF478480	AF478520
Festuca indigesta Boiss.	Spain: Granada: Sierra Nevada: Laguna Seca PC-JALR-PT 43 (UZ)	6*x*[b]	—	AF478519
Festuca longiauriculata Fuente, Ortúnez & Ferrero	Spain: Almeria: Sierra de los Filabres: Calar Alto PC-JALR-PT 59 (UZ)	2*x*[b]	AF478479	AF478518
Festuca ovina L.	Germany: Thüringen: Saale-Holzland-Kreis JM 6879 (UZ)	2*x*[a]	AF532959	AF533063
Festuca plicata Hack.	Spain: Granada: Sierra Nevada: Dornajo PC-JALR-PT 86 (UZ)	2*x*[b]	AF478483	AF478525
sect. *Aulaxyper* Dumort. (type *F. rubra* L.) ("*F. rubra* complex")				
Festuca iberica (Hack.) K. Richt.	Spain: Granada: Sierra Nevada: Borreguiles San Juan PC-JALR-PT 77 (UZ)	6*x*[c]	AY118087	AF478516
Festuca juncifolia St.-Amans	Spain: Lugo: Viveiro: Brieiro: Arenales de Area JALR 01366 (UZ)	8*x*[a]	AF478478	AF478515
Festuca nevadensis (Hack.) K. Richt.	Spain: Granada: Sierra Nevada: Dornajo PC-JALR-PT 69 (UZ)	10*x*[a]	AF478477	AF478514

Table 2. Continued.

Taxa[1]	Source	Ploidy level[2]	GenBank accession No.	
			ITS	*trn*L-F
Festuca pyrenaica Reut.	Torrecilla & Catalán (2002); Spain: Huesca: Pyrénées: Cotiella	4*x*[a]	AF303423	AF478517
Festuca rivularis Boiss.	Spain: Granada: Sierra Nevada: Borreguiles San Juan PC-JALR-PT 78 (UZ)	2*x*[a]	AF478475	AF478512
Festuca rothmaleri (Litard.) Markgr.-Dann.	Spain: Madrid: Lozoya JALR 01227b (UZ)	8*x*[c]	AF478476	AF478513
Festuca rubra L. (1)	Torrecilla & Catalán (2002); Romania	6*x*[a]	AF303422	AY118098
Festuca rubra L. (2)	Switzerland: Valais: Desses des Ferret JM 8060	6*x*[a]	AY118088	AY118099
sect. *Festuca*				
subsect. *Exaratae* St.-Yves (type *F. capillifolia* Dufour)				
Festuca borderei (Hack.) K. Richt.	Torrecilla & Catalán (2002); Spain: Huesca: Vallibierna	2*x*[a]	AF303403	AF478510
Festuca capillifolia Dufour	Torrecilla & Catalán (2002); Spain: Jaén: Cazorla	2*x*[b]	AF303419	AF478511
sect. *Eskia* Willk. p.p. (type *F. eskia* Ramond ex DC.)				
Festuca burnatii St.-Yves	Spain: Cantabria: Picos de Europa PC-PT 44 (UZ)	2*x*[a]	AY099007	AY099002
Festuca eskia Ramond ex DC.	Torrecilla & Catalán (2002); Spain: Huesca: Pyrénées: Benasque	2*x*[a]	AF303412	AF478508
Festuca gautieri (Hack.) K. Richt.	Torrecilla & Catalán (2002); Spain: Gerona: Pyrénées: Nuria	2*x*[a]	AF303414	AF478507
Festuca quadriflora Honck.	Torrecilla & Catalán (2002); France: Pyrénées: Col de Baroude	2*x*[a]	AF303413	AF478506
sect. *Pseudatropis* Krivot. (type *F. elegans* Boiss.)				
Festuca elegans Boiss.	Torrecilla & Catalán (2002); Spain: Granada: Baza	2*x*[d]	AF303406	AF478509
Vulpia C. C. Gmel. (type *V. myuros*)				
sect. *Vulpia* (type *V. myuros* (L.) C. C. Gmel.)				
Vulpia bromoides (L.) S. F. Gray	Spain: Lugo: Láncara JALR 1080 (UZ)	2*x*[e]	AF478485	AF478616

Table 2. Continued.

Taxa[1]	Source	Ploidy level[2]	GenBank accession No.	
			ITS	*trn*L-F
Vulpia ciliata Dumort. (1)	Spain: Zaragoza: Actur PC-SP 10 (UZ)	4*x*[c]	AF478486	AF478527
Vulpia ciliata Dumort. (2)	Spain: Zaragoza: Vedado de Peñaflor PC 19 (UZ)	4*x*[c]	AY118094	AY118104
Vulpia ciliata Dumort. (3)	Spain: Burgos: Solduengo: Navas de Bureba J37694 (JACA)	4*x*[c]	—	AY118105
Vulpia muralis (Kunth) Nees (1)	Spain: Zaragoza PC-SP 11 (UZ)	2*x*[c]	AF478484	AF478526
Vulpia muralis (Kunth) Nees (2)	Spain: Sevilla: Sierra Morena: Alto del Palancar PC (UZ)	2*x*[c]	AY118091	AY118102
Vulpia myuros (L.) C. C. Gmel. (1)	USA: Washington: Seattle: Lake Forest Park PC 54 (UZ)	6*x*[c]	AY118092	AY118103
Vulpia myuros (L.) C. C. Gmel. (2)	Charmet et al. (1997)	6*x*[c]	AJ240162	—
sect. *Monachne* Dumort. (type *V. fasciculata* (Forssk.) Samp.)				
Vulpia fasciculata (Forssk.) Samp. (1)	Spain: Barcelona: Vilanova SP (UZ)	4*x*[c]	AF478487	AF478528
Vulpia fasciculata (Forssk.) Samp. (2)	Torrecilla & Catalán (2002); Greece: Kikladhes: Paros	4*x*[c]	AF303402	—
Vulpia fontqueriana Melderis & Stace	Spain: Segovia: Lastras de Cuellar: Nava del Pobo JALR 16-6-2000 (UZ)	2*x*[c]	AF478488	AF478529
Vulpia membranacea (L.) Dumort.	Spain: Cádiz: Sanlucar de Barrameda: La Algaida PC 8 (UZ)	2*x*[c]	AY118090	AY118101
sect. *Spirachne* (Hack.) Boiss. (type *V. inops* Hack. (= *V. brevis* Boiss. & Kotschy))				
Vulpia brevis Boiss. & Kotschy	Cyprus: SE Nicosia. CAS (LEI)	2*x*[c]	AF478489	AF478530
sect. *Loretia* (Duval-Jouve) Boiss. (type *L. geniculata* (L.) Douval-Jouve (= *V. geniculata* (L.) Link))				
Vulpia alopecuros (Schousboe) Dumort.	Portugal: Algave: Lagos: Meia Praia CAS (LEI)	2*x*[c]	AF478491	AF487617
Vulpia geniculata (L.) Link	Spain: Sevilla: Constantina J29397 (JACA)	2*x*[c]	AF478490	AF478531
Vulpia sicula (C. Presl) Link	France: Corse: Ponte Leccia J366589 (JACA)	2*x*[f]	AY118089	AY118100

Table 2. Continued.

Taxa[1]	Source	Ploidy level[2]	GenBank accession No. ITS	GenBank accession No. *trn*L-F
sect. *Apalochloa* (Dumort.) Stace (= *Nardurus* (Bluff, Nees & Schauer) Rchb.) (type *Brachypodium tenellum* Roem. & Schult. (= *Vulpia unilateralis* (L.) Stace))				
Vulpia unilateralis (L.) Stace (1)	Spain: Zaragoza: Vedado de Peñaflor PC 18 (UZ)	2*x*[c]	AY118095	AY118106
Vulpia unilateralis (L.) Stace (2)	Spain: Huesca: Laspuña J22694 (JACA)	2*x*[g]	AY118096	AY118107
Ctenopsis De Not. (type *C. pectinella* (Delile) De Not.)				
Ctenoposis delicatula (Lag.) Paunero	Spain: Madrid: Garganta de Los Montes JALR 14-6-00 (UZ)	2*x*[c]	AF478499	AF478537
Cutandia Willk. (type *C. scleropoides* Willk. (= *C. memphitica* (Spreng.) K. Richt.))				
Cutandia maritima (L.) Barbey	Spain: Coruña: Ribeira: Arenales de Castro JALR 1050 (UZ)	2*x*[c]	AF478496	AF487618
Micropyrum Link (type *Triticum tenellum* L. (= *M. tenellum* (L.) Link))				
Micropyrum patens (Brot.) Rothm. ex Pilg.	Spain: Madrid: Cadalso de los Vidrios JALR 1194 (UZ)	2*x*[c]	AF478495	AF195885
Micropyrum tenellum (L.) Link	Spain: Segovia: Navafría JALR 14-6-00 (UZ)	2*x*[c]	AF478494	AF478534
Narduroides Rouy (type *Narduroides salzmanii* (Boiss.) Rouy)				
Narduroides salzmanii (Boiss.) Rouy	Spain: Madrid: Dehesa de Arganda JALR 01007 (UZ)	2*x*[c]	AF478497	AF478535
Psilurus Trin. (type *P. nardoides* Trin. (= *P. incurvus* (Gouan) Schinz & Thell.))				
Psilurus incurvus (Gouan) Schinz & Thell.	Spain: Huesca: Estopiñan J 236098 (JACA)	4*x*[b]	AF478493	AF478533
Wangenheimia Moench (type *W. disticha* Moench (= *W. lima* (L.) Trin.))				
Wangenheimia lima (L. Trin.)	Spain: Zaragoza: Vedado de Peñaflor PC-SP-PT 17 (UZ)	2*x*[f]	AF478498	AF478536
Outgroups:				
Festuca L. subg. *Drymanthele* Krechetovich & Bobrov (type *F. sylvatica* Pollich (= *F. altissima* All.))				
Festuca altissima All.	Torrecilla & Catalán (2002): France: Pyrénées: Aspe	2*x*[a]	AF303411	AF478505

Table 2. Continued.

Taxa[1]	Source	Ploidy level[2]	GenBank accession No. ITS	GenBank accession No. *trn*L-F
subg. *Schedonorus* (P. Beauv.) Peterm. (type *F. elatior* L. (= *F. arundinacea* Schreb.))				
sect. *Schedonorus* (P. Beauv.) W. D. J. Koch (type *F. elatior* L. (= *F. arundinacea* Schreb.))				
Festua pratensis Huds.	Torrecilla & Catalán (2002); England: Wiltshire: Calne	2*x*[a]	AF303421	AF478503
Lolium L.				
Lolium perenne L.	Torrecilla & Catalán (2002); England (cv.)	2*x*[j]	AF303401	AF478504
Dactylis L.				
Dactylis glomerata L.	Spain: Zaragoza: Moncayo PC-PT 97 (UZ)	4*x*[j]	AF393013	AF533028
Poa L.				
Poa infirma Kunth	Torrecilla & Catalán (2002); Spain: Zaragoza: La Jota	2*x*[j]	AF393012	AF488773
Puccinellia Parl.				
Puccinellia distans (L.) Parl.	Spain: Navarra: Lazagurría J207897 (JACA)	6*x*[j]	AF393012	AF488773
Sesleria Scop.				
Sesleria argentea (Savi) Savi	Spain: Navarra: Araxes PC 21 (UZ)	4*x*[j]	AF532931	AF533030
Secale L.				
Secale cereale L.	Torrecilla & Catalán (2002); USA (cv.)	2*x*[j]	AF303400	AF478501
Brachypodium P. Beauv.				
Brachypodium distachyon (L.) P. Beauv.	Torrecilla & Catalán (2002); Slovenia: Ljubljana	2*x*[k]	AF303399	AF478500

[1] Numbers in parentheses correspond to different accessions of the same taxon.

[2] Data sources: a, Markgraf-Dannenberg (1980); b, Fuente et al. (2001); c, Al-Bermani et al. (1992); d, Ferrero & Fuente (1996); e, Cotton & Stace (1976); f, Stace & Cotton (1973); g, Cotton & Stace (1977); h, Tutin (1980); i, Stace (1980); j, Kerguélen (1999); k, Torrecilla & Catalán (2002).

genetic relationships via long-branch-attraction and/or increased levels of homoplasy (Bousquet et al., 1992; Gaut et al., 1992, 1996, 1997). Because *Vulpia*, the fine-leaved *Festuca* and the related ephemerals constitute a case study with much diversity of annual and perennial grass lineages, we have conducted relative rate tests of nucleotide substitutions to clarify the selection of adaptive patterns that may have impacted each different lineage (Gaut et al., 1997).

Materials and Methods

Taxa sampled and sequence data

Sampling of representatives of *Vulpia*, the six related annual genera, and the fine-leaved *Festuca* was accomplished by collecting fresh leaves and herbarium vouchers. A total of 57 samples corresponding to 52 taxa were incorporated into this study. Morphologically variable taxa were sequenced two (*Vulpia muralis, V. fasciculata, V. unilateralis, F. rubra*) or three times (*V. ciliata*). Eighteen of these samples that were previously included in the ITS study of Torrecilla and Catalán (2002) were sequenced for the *trn*L-F region and used to complete the sampling of the studied species. One *Vulpia myuros* ITS sequence deposited by Charmet et al. (1997) in Genbank was incorporated into the study. The full list of taxa with indications of names, authorities, localities, herbarium vouchers, Genbank accession numbers, and ploidy levels is presented in Table 2.

The sampling spectrum covered representatives from the five recognized sections of *Vulpia* (18 samples), the fine-leaved *Festuca* (24), *Micropyrum* (2), and one sample each from *Ctenopsis, Wangenheimia, Psilurus, Narduroides*, and *Cutandia*. Three representatives of the "broad-leaved" fescues, *Festuca pratensis* (*Festuca* subg. *Schedonorus*), *F. altissima* (*Festuca* subg. *Drymanthele*), and *Lolium perenne* (*Lolium*), and one representative each from *Dactylis, Poa, Puccinellia, Sesleria* (Poeae), *Secale* (Triticeae), and *Brachypodium* (Brachypodieae) were also studied (Table 2).

DNA isolation followed the same procedures stated in Torrecilla and Catalán (2002) implemented in some cases with the help of the DNAeasy Plant Mini Kit (QIAGEN). Amplification of the ribosomal ITS region (ITS1-5.8S-ITS2) and further sequencing were performed as indicated in Torrecilla and Catalán (2002) using in both cases the external primers KRC (forward) and ITS4 (reverse). PCR amplification and sequencing of the *trn*L-F region was conducted using either the external pair primers "c" and "f" (Taberlet et al., 1991), or the combined pair "fern" (forward primer: 5′-GGCAGCCCCCARATTCAGGGRAACC-3′) (S. Russell, pers. comm.) and "f" (reverse). 50 μl reactions were prepared with 5 μl 10× buffer, 3 μl $MgCl_2$ (50 mM), 4 μl dNTP (10 mM), 1 μl primer 1 (20 μM), 1 μl primer 2 (20 μM), 34.7 μl ddH_2O, 0.3 μl Taq (1.5 units), and 1 μl DNA; the reaction mixtures were subjected to one denaturing cycle of 1 min. at 94°C, 35 cycles of a 15 sec. denaturing step at 94°C, 30 sec. annealing step at 45°C, and 1 min. elongation step at 72°C, plus one 7 min. termination cycle at 72°C. The amplified products were purified using the QIAgel extraction kit (QIAGEN). Purified products were then sequenced with the ABI PRISM Dye Terminator Cycle Sequencing Ready reaction kit (Perkin Elmer) and electrophoresed in an ABI Prism 377 automated sequencer.

The direct and reverse sequences of each sample were compared and corrected using the program Chromas, obtaining the respective consensus sequences. All chloroplast *trn*L-F samples and most ITS rendered a unique sequence; however, some polymorphic positions were detected in a few ITS samples. Those sites were coded as polymorphisms using the ambiguity IUPAC symbols. A total of 38 new ITS sequences and 57 new *trn*L-F sequences of *Festuca, Vulpia, Wangenheimia, Ctenopsis, Micropyrum, Narduroides, Psilurus, Cutandia, Lolium, Dactylis, Poa, Puccinellia, Sesleria, Secale*, and *Brachypodium* have been deposited in GenBank (Table 2). All but 1 (*Festuca indigesta* subsp. *indigesta*) of the 52 taxa studied have been sequenced for both the ITS and the *trn*L-F region. A partial sequence of the ITS region of *Festuca nevadensis* (ITS1 spacer, 5.8S gene) was included in the analysis.

Each separate set of ITS and *trn*L-F sequences was first aligned using the algorithm of the program ClustalX (Thompson et al., 1994) and then adjusted manually using the options of the program Se-Al v. 1.0 alpha 1 (Rambaut, 1996). The boundaries of the ITS region (ITS1-5.8-ITS2) were determined according to those established by Hsiao et al. (1995) for the Pooideae; those of the *trn*L-F region (*trn*L intron-*trn*L 3′exon-*trn*L-F spacer) were established according to the chloroplast map of *Oryza sativa* (Hiratsuka et al., 1989). Gap indels were coded as binary characters by their presence/absence (0–1 matrix). Only those gaps that were unambiguous and potentially informative (Torrecilla & Catalán, 2002) were added to their correspondent sequence matrix and used for phylogenetic analysis.

PHYLOGENETIC RECONSTRUCTION, RATE ESTIMATION, AND SEQUENCE DIVERSITY

Phylogenetic analyses were based on both Parsimony and Bayesian inference approaches as a means to compare topologies obtained from cladistic and nucleotide substitution-model-based methods. The ITS and *trn*L-F data sets were constructed and subjected to separate analyses. A first set of searches was carried out by both excluding and including polyploid taxa from the analyses with the intention of clarifying the placement of the polyploid lineages with respect to their potential ancestral diploids by superimposing the polyploids on the diploid-based trees. A second round of analyses was conducted excluding gap characters with the aim of evaluating the phylogenetic signal and influence that ITS and *trn*L-F indels could have in the final trees. Finally, a third seach was accomplished exclusively with the ITS data set excluding the highly variable sequence of *Cutandia maritima* from the analysis (see Results). All the searches that were conducted exclusively with the diploid data sets resolved the same topologies as those conducted with the complete data sets (diploids and polyploids included) for their common taxa (diploid) and showed similar levels of support for their respective clades; therefore, only trees obtained from the complete data matrices will be shown here. ITS trees were the same when gap characters were either included or excluded from the analyses; however, an increased lack of resolution was found for some lineages in the *trn*L-F parsimony-based tree when one informative gap indel was removed from analyses (see Results). Exclusion of *Cutandia maritima* from the ITS data set did not alter the resulting topologies or their respective levels of support.

Cladistic analyses were performed with Paup* ver. 4.0 beta 10 (Swofford, 2002) following the parsimony criterion. Each data matrix was separately subjected to two heuristic search strategies aimed to find putative isles of equally parsimonious trees. All most parsimonious trees obtained from these separate searches (search #1: closest, TBR, MULPARS ON; search #2: random-order-entry of 10,000 replicates, TBR, MULPARS OFF, saving no more than 5 trees of score > 10 per replicate) were used to compute the final strict consensus tree. Bootstrap support for the best trees found under the parsimony criterion was estimated through 10,000 replicates (Felsenstein, 1985). The TBR-M (Tree Bisection Reconstruction swapping, MULPARS OFF) strategy of DeBry and Olmstead (2000) was applied for these bootstrap searches in order to get accurate bootstrap values while reducing computational time.

A Bayesian inference search was later performed for the separate ITS and *trn*L-F data matrices using Mr. Bayes 3.0 beta 3 (Huelsenbeck & Ronquist, 2002). A test of goodness of fit for 56 nucleotide substitutions models was previously conducted on each individual data set using the likelihood ratio test statistic included in the program Model Test ver. 3.06 (Posada & Crandall, 1998) that selects the best substitution model for the given data. The estimated optimal substitution model for each separate data set was then imposed in the subsequent Bayesian analyses. The General-Time-Reversibility model with 6 substitution types was the available option in Mr. Bayes 3.0 for those optimal models (see Results). Separate searches were conducted for each independent data matrix under the GTR model (4 gamma rate categories) allowing the program to estimate the likelihood parameters relative to nucleotide frequencies, nucleotide substitution rates, and gamma shape (proportion of invariable sites was set to zero concordantly with the best substitution models selected by ModelTest for each independent ITS and *trn*L-F data set).

Bayesian analyses were first performed through 1,000,000 trees generated by the Markov chain Monte Carlo (MCMC) sampling trees every 100 generations; phylogenies sampled from their posterior probability distribution were then examined for stationarity in their likelihood values. Sampled points from generations that did not reach a stable equilibrium value (Leaché & Reeder, 2002) were eliminated using the burn-in option of Mr. Bayes 3.0. New Bayesian searches of 1,000,000 MCMC generations were conducted for each separate data set; topologies sampled from these new searches were used to construct the respective 50% Majority-Rule consensus trees where the percentage of times a clade is recovered is interpreted as an estimation of robustness.

The Incongruence Length Difference (ILD) test of Farris et al. (1994) was calculated to determine if the two data sets (ITS and *trn*L-F) differ significantly from random partitions of the same size. The TBR-M approach of DeBry and Olmstead (2000) was applied to compute the significance values of the test replicates. Although significance was achieved from this ILD test (see Results) we decided to unite the two data matrices onto a combined one and to conduct further phylogenetic analyses to explore the resolution obtained from the combined analysis and to evaluate topological incongruences for lineages differently supported in the separate and combined trees. The heuristic and

bootstrap analyses of the combined data matrix were performed using the same strategies described above for the parsimony analysis. Bayesian inference was also conducted on the combined data set following the same procedure as for the independent data matrices but imposing separate substitution models for each partition in the simultaneous analysis using the options provided in Mr. Bayes 3.0.

Consensus topologies recovered from the above-mentioned analyses showed differences in branch lengths for several lineages (see Results). In order to investigate the differential rates of evolution that may have been followed by these lineages, we conducted relative rate tests of nucleotide substitutions (see Results) between different sequences or groups of sequences using RRTree 1.1 (Robinson et al., 1998; Robinson & Huchon, 2000). This program constrains the test between lineages or groups of sequences (or between pairs of individual sequences), which are weighted by a given topology, using a close outgroup as reference (Robinson & Huchon, 2000). Rates of substitutions were compared and tested between the main lineages or groups of lineages resolved by the Bayesian phylogenetic analyses in the separate ITS and *trn*L-F trees. The test was restricted to the ingroup taxa using *Festuca pratensis* (*Festuca* subg. *Schedonorus*), a member of the close "broad-leaved" *Festuca* clade, as outgroup. Comparisons were also extended to pairs of individual sequences within and across lineages with the aim of analyzing the rates of substitutions for taxa that showed substantial differences in branch lengths with respect to other consectional or close taxa. The Kimura 2-parameter model was chosen to estimate the rates of substitution between the ITS and *trn*L-F non-coding sequences.

Pairwise comparisons between all sequences detected a few cases, mostly related to the ITS data set, where individual sequences showed increased rates of substitutions with respect to other consectional, conspecific, or close lineages (see Results). In order to evaluate if these lineages evolved more rapidly than other lineages or could represent potential heterologous samples arbitrarily amplified from direct PCR reactions we analyzed the % G + C content of their ITS1 regions, which showed to be the most variable in all the studied taxa, and estimated the minimum-free energies (MFE) of folding of their respective RNA transcripts using the program MFOLD ver. 3.1 (Zuker, 1989; Mathews et al., 1999; Zuker et al., 1999). Folding calculations were set to the default parameters for RNA sequences (37°C, 5% of thermodynamic optimatility) and were made at the M. Zuker web site (http://www.bioinfo.rpi.edu/applications/mfold/old/rna/form1.cgi).

Results

DNA Sequences

The ITS sequences of the studied taxa ranged from 592 bp (*Dactylis glomerata*) to 613 bp (*Brachypodium distachyon*), or 599 bp (*Vulpia sicula*) to 610 bp (*Vulpia fontqueriana, V. membranacea, V. unilateralis, Psilurus incurvus*) within the ingroup taxa. The aligned data matrix consists of 634 positions after the introduction of gaps, which ranged from 1 bp to 4 bp. Three hundred fifty-two out of 634 nucleotide positions are variable (55% of the total); of these 147 are located in the ITS1 region (23%), 38 in the 5.8S gene region (6%), and 167 in the ITS2 region (26%). Of the variable positions 208 are potentially informative (33% of the total) (94 (15%) in the ITS1, 19 (3%) in the 5.8S gene, 95 (15%) in the ITS2).

The *trn*L-F data matrix ranged from 779 (*Puccinellia distans*) to 908 (*Secale cereale*) or 819 bp (*Festuca rothmaleri*) to 848 bp (*Psilurus incurvus, Micropyrum tenellum*) within the ingroup taxa. The aligned data matrix is made of 1022 positions after the introduction of gaps that varied from 1 bp to 32 bp (a 64 bp deletion in *Puccinellia distans*). The rate of variability and potential phylogenetic informativeness of the chloroplast *trn*L-F region is lower than that of the nuclear ITS region for a similar set of taxa. In the *trn*L-F region 323 out of 1022 positions are variable (32% of the total), and of these 164 (16%) are located in the *trn*L intron, 11 (1%) are located in the *trn*L 3′ exon, and 148 (15%) in the *trn*L-F spacer. Of 323 total variable sites, 131 are potentially informative (12.5% of the total) (76 (7.3%) in the *trn*L-F intron, 2 (0.2%) in the *trn*L 3′exon, and 53 (5%) in the *trn*L-F spacer).

Phylogenetic Analysis

The ITS Data Set

The first heuristic search found one island of 213,592 equally parsimonious trees that were 950 steps long, CI = 0.469 excluding uninformative characters, RI = 0.610. The second strategy rendered 6631 equally parsimonious trees of the same length and statistics as the previous ones. The strict consensus tree of all these most parsimonious trees is shown in Figure 1.

A monophyletic *FEstuca* sensu stricto + *Vulpia* + Related Ephemerals (FEVRE) group that encompasses *Festuca* sects. *Eskia, Festuca, Aulaxyper* and subsection *Exaratae*; *Vulpia* sects. *Vulpia, Monach-*

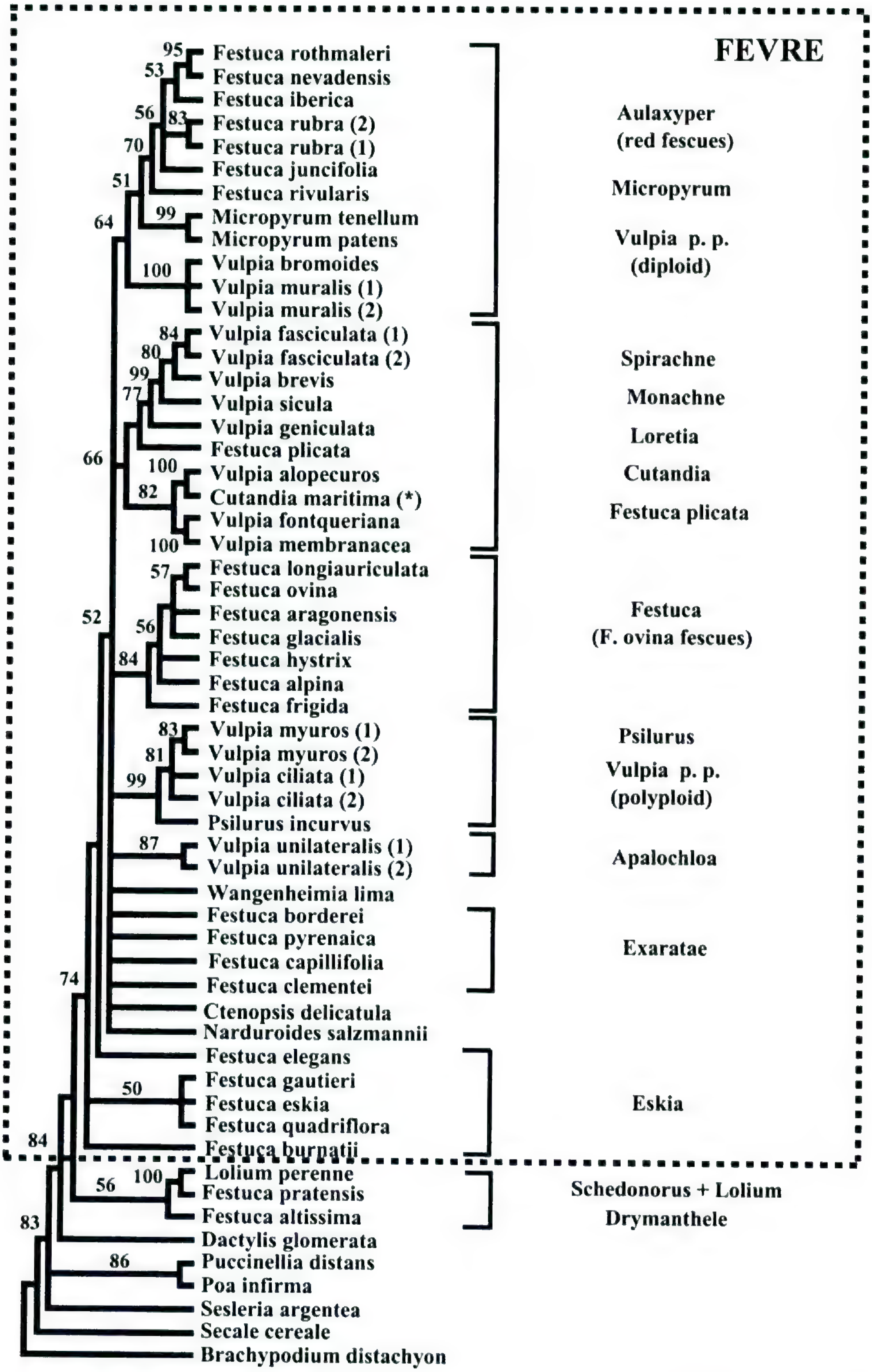

Figure 1. ITS tree: strict consensus tree of 213,592 equally parsimonious trees (L = 950, CI = 0.469 excluding uninformative characters, RI = 0.610). Bootstrap percentage is indicated on the corresponding branches. Asterisk corresponds to a highly variable sequence of *C. maritima* that was both included and excluded from analyses (see Results and Discussion). Species numbers correspond to different accessions of the same taxon (see Table 2).

ne, *Spirachne*, *Loretia*, and *Apalochloa*; and *Psilurus*, *Ctenopsis*, *Wangenheimia*, *Cutandia*, *Micropyrum*, and *Narduroides* is obtained when *Brachypodium distachyon* is used to root the trees. The first diverging lineages of the FEVRE group are those corresponding to *Festuca* sect. *Eskia*. This taxon forms a non-resolved basal assemblage of five species (see Fig. 1). The core of the FEVRE taxa is also unresolved at the base; five clades collapse with seven single taxa in a polytomy. These terminal taxa are those belonging to *Festuca* subsect. *Exaratae* (*F. borderei*, *F. capillifolia*), *F. clementei*, *F. pyrenaica*, *Narduroides*, *Wangenheimia*, and *Ctenopsis*. Of the five resolved clades one represents the Aulaxyper + Micropyrum + diploid Vulpia (diploid *Vulpia* sect. *Vulpia*) lineage. *Micropyrum* is resolved as sister of *Festuca* sect. *Aulaxyper*, though this relationship is poorly supported; this group is respectively sister to the diploid *Vulpia* sect. *Vulpia* clade. High bootstrap support is shown for the separate lineages diploid Vulpia (bs 100), Micropyrum (bs 99), and the sister taxa *Festuca nevadensis* + *F. rothmaleri* (bs 95). The second clade is resolved into two diverging lineages of intermixed representatives of *Vulpia* sects. *Spirachne*, *Monachne*, and *Loretia* plus *Cutandia* and *Festuca plicata*. The ((Vulpia alopecuros + Cutandia), (Vulpia membranacea + V. fontqueriana)) subclade is well supported, whereas the ((Vulpia brevis + V. fasciculata), V. sicula), V. geniculata) subclade is mostly robust throughout. A third clade is that of the *Festuca* taxa with relatively high bootstrap support (bs 84) but little internal resolution. A fourth Psilurus + polyploid Vulpia (polyploid *Vulpia* sect. *Vulpia*) clade is also highly supported (bs 99); *Psilurus* is resolved as the closest relative of a clade of *Vupia* representatives where two sister accessions of *V. myuros* (bs 83) collapse in a polytomy with two representatives of *V. ciliata* (bs 81). The fifth clade is that of two representatives of *Vulpia unilateralis* (bs 87) (*Vulpia* sect. *Apalochloa*).

Model Test found TrN + G to be the best substitution model for the ITS data matrix. The Bayesian analysis conducted under the GTR model (nst = 6, pinv = 0) sampled 8927 trees that reached a stable likelihood value after the burn-in of 1074 trees; the 50% majority rule consensus tree of all sampled trees is shown in Figure 2. The phylogenetic relationships recovered in this tree are similar to those shown in the parsimony-based tree for the best supported groups (Fig. 1), notably those corresponding to the basal *Eskia* group, and to the internal clades Aulaxyper + Micropyrum + diploid Vulpia, Spirachne + Monachne + Loretia + Cutandia + F. plicata, Festuca, and Psilurus + polyploid Vulpia. The Apalochloa clade is nested within a clade of ephemeral taxa (including *Wangenheimia*, *Narduroides*, and *Ctenopsis*) in this Bayesian tree.

The trn*L-F Data Set*

The first heuristic strategy found one island of 1,694,665 equally parsimonious trees that were 533 steps long, CI = 0.610 excluding uninformative characters, RI = 0.778. The second search rendered 3838 equally parsimonious trees of the same length and statistics as previously. The strict consensus tree of all these most parsimonious trees is shown in Figure 3. The *trn*L-F strict consensus topology shows a slightly higher resolution for the deep internal branches of the core taxa than that of the ITS strict consensus topology (Fig. 1) though they remain poorly supported. The consensus topology was less resolved for representatives of *Vulpia* sects. *Spirachne*, *Monachne*, and *Loretia* and related ephemerals and for those of *Festuca* subsect. *Exaratae* and allies when gap characters were excluded from analysis (results not shown). Four of the five gap characters constitute additional markers for clades already supported by substitution changes; however, a fifth gap shared by representatives of *Vulpia* sects. *Spirachne*, *Monachne*, *Loretia*, and *Apalochloa* plus *Cutandia*, *Festuca plicata*, *Festuca* subsect. *Exaratae*, *F. pyrenaica* and *F. clementei* is the only character that supports the monophyly of this group in the parsimony-based tree (Fig. 3). Nonetheless, the Bayesian inference, which is solely based on nucleotide sequences (Fig. 4), recovers a similar topology to the parsimony based one.

The *trn*L-F data set also confirms the monophyly of the FEVRE group, which is supported by a high bootstrap value (bs 94) (Fig. 3). Within this clade representatives of *Festuca* sect. *Eskia* are paraphyletic and basal to a core of fine-leaved fescues, *Vulpia*, and related annual genera (Fig. 3). In this *trn*L-F topology, *Festuca burnatii* and *F. quadriflora* separate earlier from the common ancestor but are unresolved, being followed by the divergence of the remaining *Eskia* taxa (*F. eskia*, *F. gautieri*, *F. elegans*) that collapse in a polytomy and are sister to the rest. The core of the FEVRE taxa is formed by three lineages that collapse in a further polytomy. The best resolved lineage is the one that encompasses the "*rubra* and *ovina*" fescues and their allies (bs 92). Within this group the Aulaxyper + diploid Vulpia clade is well supported (bs 97). The clade is sister to the Festuca + Wangenheimia one (bs 92) where the Festuca subclade shows a high bootstrap value (bs 99). *Narduroides* is resolved as

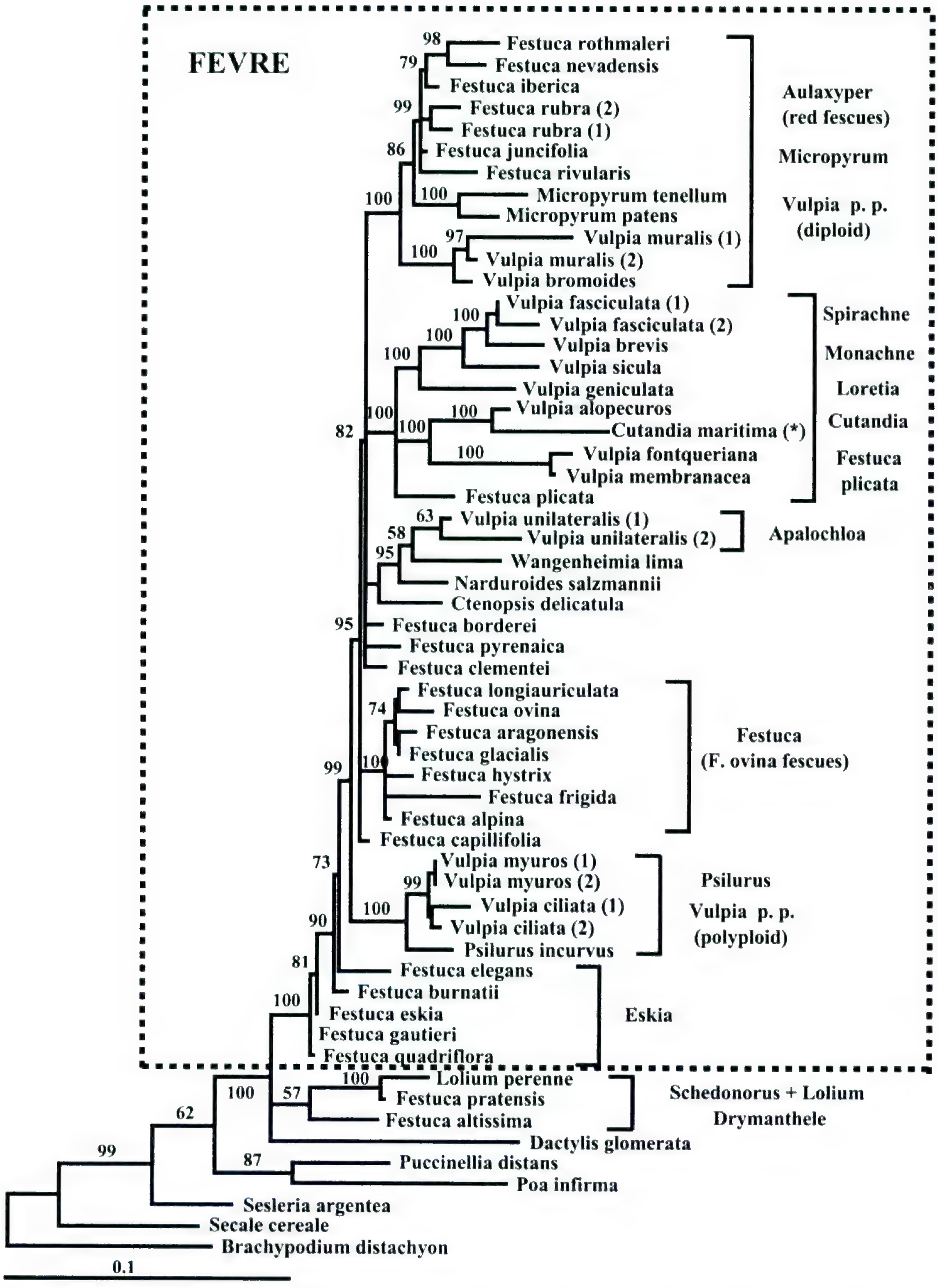

Figure 2. ITS tree: Bayesian 50% Majority-Rule (MR) consensus tree of 8927 trees. Posterior probability percentage is indicated on the corresponding branches. Asterisk corresponds to a highly variable sequence of *C. maritima* that was both included and excluded from analyses (see Results and Discussion). Species numbers correspond to different accessions of the same taxon (see Table 2).

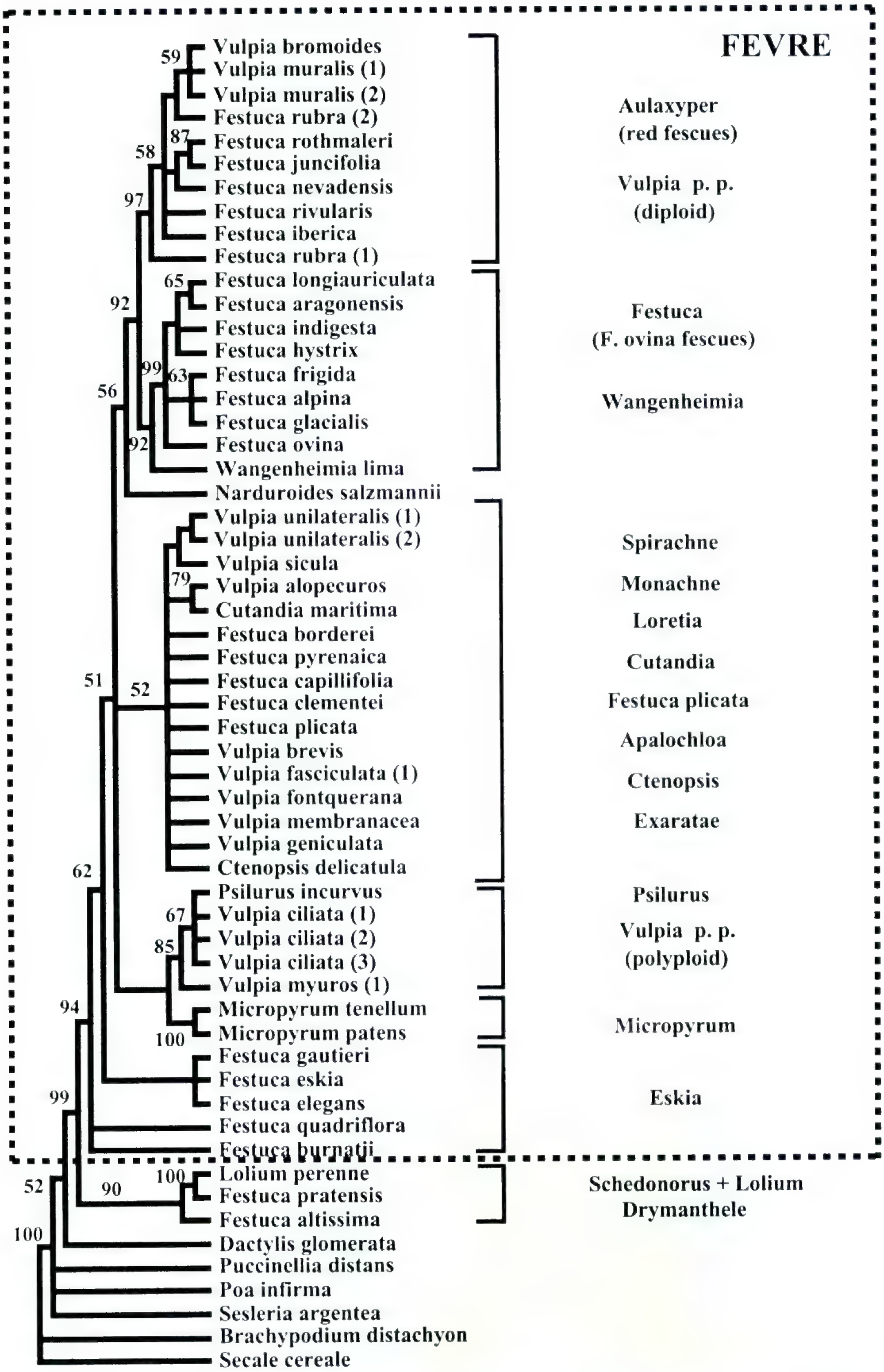

Figure 3. *trn*L-F tree: strict consensus tree of 1,694,665 equally parsimonious trees (L = 533, CI = 0.610 excluding uninformative characters, RI = 0.778). Bootstrap percentage is indicated on the corresponding branches. Species numbers correspond to different accessions of the same taxon (see Table 2).

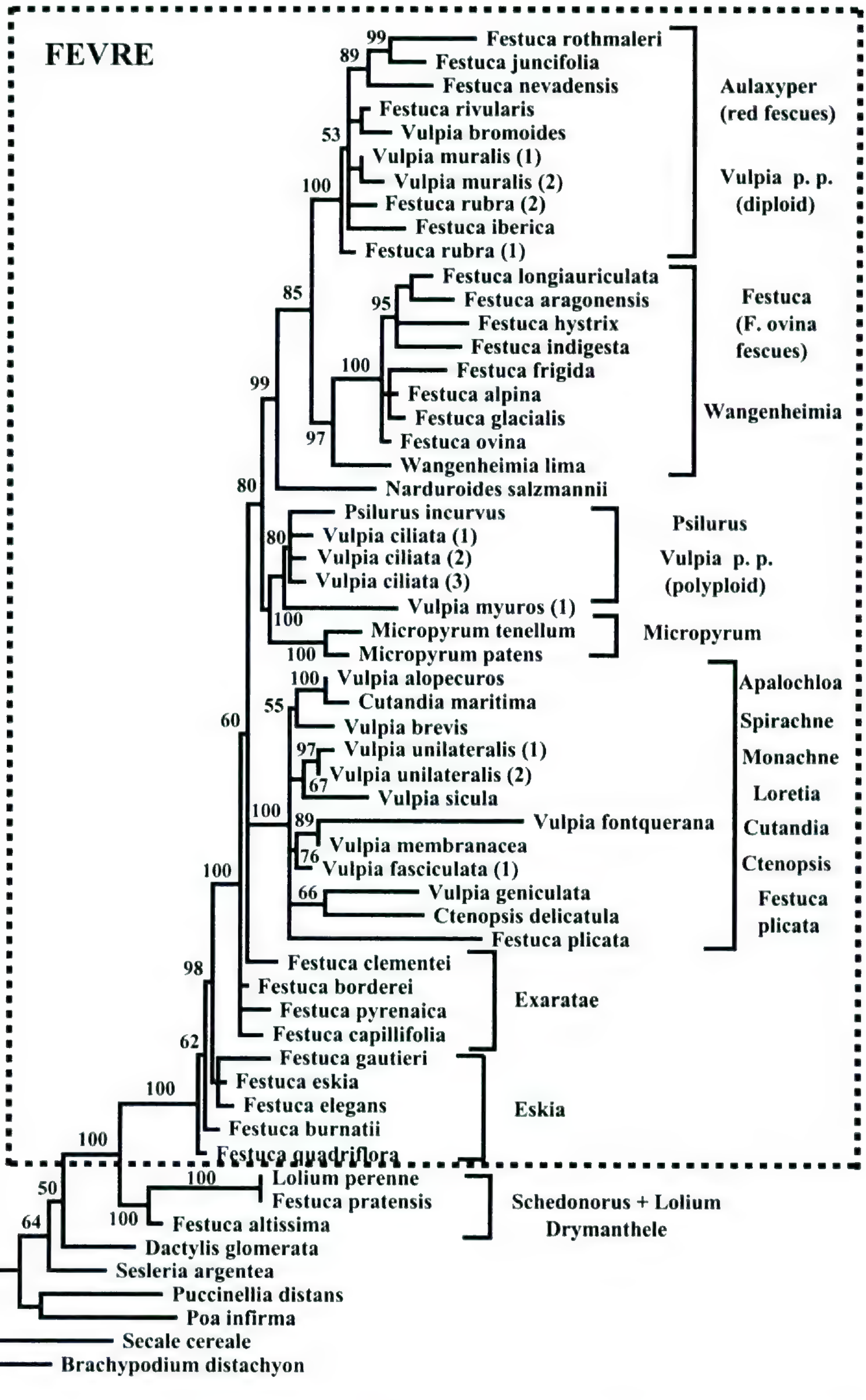

Figure 4. *trn*L-F tree: Bayesian 50% MR consensus tree of 9890 trees. Posterior probability percentage is indicated on the corresponding branches. Species numbers correspond to different accessions of the same taxon (see Table 2).

the sister taxon of the former groups but this relationship shows low bootstrap support (bs 56) (Fig. 3). A second lineage of Psilurus + polyploid Vulpia shows relatively high support (bs 85); *Vulpia myuros* is resolved as sister to an unresolved clade of *Psilurus* and *Vulpia ciliata* representatives with low bootstrap support (bs 67). A highly robust Micropyrum clade includes the sister taxa *M. tenellum* and *M. patens*. This clade is resolved as sister to the Psilurus + polyploid Vulpia lineage though this relationship lacks bootstrap support. The third lineage includes representatives of *Vulpia* sects. *Spirachne*, *Monachne*, *Loretia*, and *Apalochloa*, *Cutandia*, *Ctenopsis*, *Festuca plicata*, and *Festuca* sect. *Exaratae* (*F. borderei*, *F. capillifolia*) plus *F. clementei* and *F. pyrenaica*. This group is poorly resolved and not strongly supported except for the relationships of the sister taxa Vulpia alopecuros + Cutandia maritima (bs 79). *Vulpia unilateralis* (*Vulpia* sect. *Apalochloa*) is resolved here as sister to *Vulpia sicula* though their relationship is not supported (Fig. 3).

The goodness of fit test of ModelTest indicated K81uf + G as the best substitution model for the *trn*L-F data matrix. The Bayesian analysis conducted under the GTR model (nst = 6, pinv = 0) sampled 9890 trees that reached a stable likelihood value after the burn-in of 111 trees; the 50% majority-rule consensus tree of all sampled trees is shown in Figure 4. The phylogenetic relationships recovered by this analysis are congruent with those based in the parsimony approach, as manifested in the two topologies depicted in Figures 3 and 4. All groups except the unresolved *Festuca* sect. *Exaratae* taxa plus *F. clementei* and *F. pyrenaica* show congruence in both parsimony and Bayesian trees.

*The Combined ITS/*trn*L-F Data Set*

Parsimony strict consensus topologies and Bayesian 50% majority-rule consensus trees obtained from the two separate data sets, ITS and *trn*L-F, were coincident for several groups, especially for the best supported lineages Aulaxyper + diploid Vulpia, Festuca, Psilurus + polyploid Vulpia, and Spirachne + Monachne + Loretia + Cutandia + F. plicata and for the basal position of section *Eskia* (Figs. 1–4). These results indicate that both the nuclear and the chloroplast genomes recover a similar phylogenetic signal for most of the studied taxa. Incongruences between the ITS and *trn*L-F trees refer to the distinct placement of *Vulpia* sect. *Apalochloa*, as well as *Wangenheimia*, *Micropyrum*, and *Narduroides*.

To clarify the evolutionary relationships of those groups and to improve the resolution of the final tree we decided to unite both data matrices into a combined one and conduct further simultaneous phylogenetic analysis on the enlarged data set. A combined ITS/*trn*L-F data matrix was made of 55 samples that were sequenced for the two molecules; the ILD test of Farris et al. (1994) carried out on this ITS/*trn*L-F data matrix indicates that the two data sets are significantly different from two random partitions of the same size as the original data matrices (1000 replicates; $P = 0.001$). Arguments about the validity that heterogeneity detected by the test between sequence data matrices may have in terms of their combinability have been various (Davis et al., 1998; Johnson & Soltis, 1998; Yoder et al., 2001; Barker & Lutzoni, 2002). Davis et al. (1998), Yoder et al. (2001), and Barker and Lutzoni (2002) considered the ILD test an inappropriate method to test for the combination of data partitions for simultaneous analyses; the latter authors further demonstrated the poor predicting value shown by the ILD test for data set combinability intended to increase phylogenetic accuracy even at critical values as low as $P = 0.001$.

The first heuristic search found one island of 577 equally parsimonious trees that were 1488 steps long, CI = 0.503 excluding uninformative characters, RI = 0.644. The second strategy rendered 686 equally parsimonious trees of the same length and statistics that enlarged the spectrum of equally parsimonious trees. The strict consensus tree of all these most parsimonious trees is shown in Figure 5.

The strict consensus ITS/*trn*L-F tree depicted in Figure 5 is resolved for the main FEVRE groups; this FEVRE clade shows strong bootstrap support (bs 100) and resolution is obtained here for the divergence of the basal section *Eskia* taxa (Fig. 5) and for the branching of some internal core FEVRE lineages. The two representatives of *Vulpia unilateralis* join in a well supported monospecific Apalochloa clade (bs 99) that is resolved as sister to *Ctenopsis* and then to the Spirachne + Monachne + Loretia + Cutandia + F. plicata clade though none of these relationships is supported. The Micropyrum taxa also join in a congeneric clade that shows strong bootstrap support (bs 100). The combined ITS/*trn*L-F tree shows only a partial resolution for the relationships between the core FEVRE groups. The best resolved lineage is that of the Aulaxyper + diploid Vulpia and the Festuca + Wangenheimia groups, which link together in a clade that is sister to *Narduroides*; however, these relationships lack bootstrap support. Internal resolution is absent for the remaining lineages, except for a clade that shows a paraphyletic basal divergence of

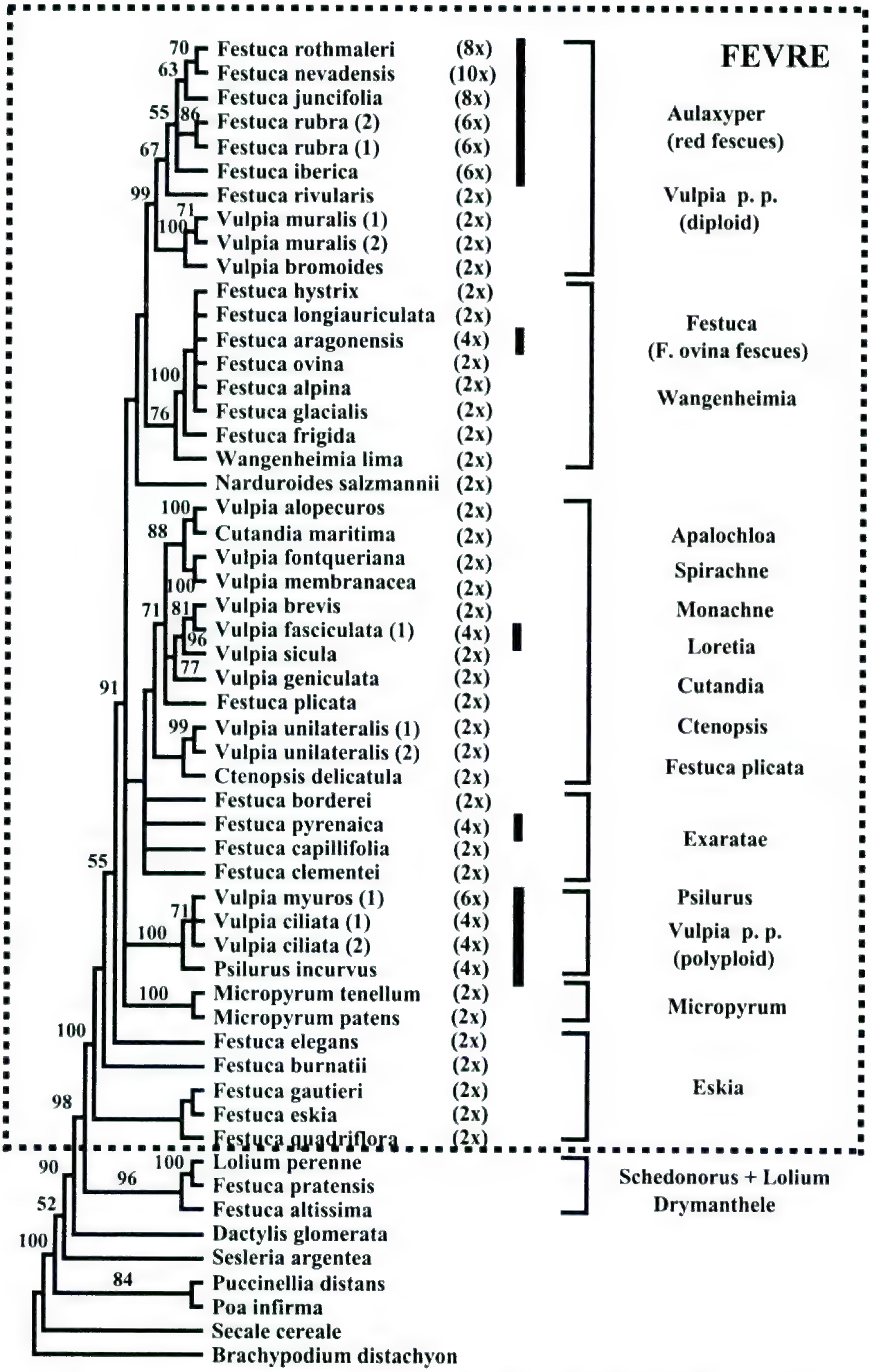

Figure 5. Combined ITS/*trn*L-F: strict consensus tree of 686 equally parsimonious trees (L = 1488, CI = 0.503 excluding uninformative characters, RI = 0.644). Bootstrap percentage is indicated on the corresponding branches. Species numbers correspond to different accessions of the same taxon (see Table 2). Ploidy levels are mapped into the tree; black bars correspond to polyploid lineages.

the *Festuca* subsect. *Exaratae* taxa plus *F. pyrenaica* and *F. clementei* from the topology for the core group of *Vulpia* taxa and their allies (Fig. 5).

The Bayesian simultaneous analysis conducted under the GTR model (nst = 6, pinv = 0) sampled 9643 trees that reached a stable likelihood value after the burn-in of 358 trees; the 50% majority rule consensus tree of all sampled trees is shown in Figure 6. Relationships recovered by this analysis are mostly congruent with those based in the parsimony approach; however, a polytomic assemblage of *Festuca* subsect. *Exaratae* taxa plus *F. pyrenaica* and *F. clementei* taxa are resolved here as the basal lineages of the core FEVRE group, whereas the Psilurus + polyploid Vulpia clade and the Micropyrum clade collapse in a polytomy with the "*Festuca rubra* and *ovina*" group plus allies.

Rates of Substitutions and Sequence Diversity between FEVRE Lineages

Values and levels of significance of the relative-rate tests calculated between the main FEVRE lineages for the separate ITS and *trn*L-F sequences are shown in Table 3. Rates of substitutions vary more for the ITS sequences than for the *trn*L-F ones, reflecting the less constrained nature of the ribosomal nuclear region compared to the conserved one of the chloroplast genome. Overall, perennial lineages show significant lower rates of substitution than the annual ones for both ITS and *trn*L-F sequences; however, most of these low rates are contributed to by representatives of the *Eskia* group, which show significant differences to almost all other FEVRE lineages for both genomic regions. When the *Eskia* taxa are removed from the test, the core FEVRE perennial lineages evolve, in general terms, at a slower pace than the core FEVRE annual ones but the differences are not significant. Pairwise comparisons between individual sequences show *Festuca elegans* to be the fastest evolving lineage within the otherwise slow evolving assemblage of *Eskia* taxa (results not shown).

The core FEVRE perennial groups also show marked differences in their respective substitution rates; the *Exaratae* group evolves slower, followed by the intermediate rate of the *Festuca* lineage and the more rapidly evolving rates of the *Aulaxyper* lineage (Table 3). Significant differences in substitution rates between the *Exaratae* group and the annuals occur for both the ITS and the *trn*L-F sequences though they are restricted only to the ITS set in several *Festuca* to ephemeral-groups comparisons. The *Aulaxyper* lineage shows higher substitution rates than those of the other perennial groups and evolves only slightly slower than most of the annual lineages except for the *Loretia* assemblage ITS sequences. This group evolves faster but not significantly more so than the red fescues if *Cutandia maritima* is excluded from the analysis (Table 3) (see Discussion). Pairwise comparisons between individual sequences found *F. rothmaleri* to be a fast-evolving lineage within the *Aulaxyper* group with rates significantly higher than those of other consectional taxa like *F. juncifolia* and *F. rivularis* in both ITS and *trn*L-F sequences. Similarly, *F. frigida* also shows significant higher substitution rates than those of the remaining cosectional *Festuca* taxa for the ITS sequences and than those of *F. alpina* and *F. clementei* for the *trn*L-F sequences (results not shown).

Within the group of FEVRE annuals the *Loretia* assemblage and *Ctenopsis delicatula* are the most rapidly evolving lineages with respect to the chloroplast *trn*L-F sequences, being significantly faster than the *Apalochloa*, *Micropyrum*, and *Wangenheimia* lineages and than the *Apalochloa*, *Micropyrum*, and *Psilurus* + polyploid *Vulpia* groups respectively (Table 3). The *Loretia* group also evolves significantly faster than the diploid *Vulpia* and the *Narduroides* lineages for the ITS sequences if *Cutandia maritima* is included in the group but shows no significant differences to those lineages if this taxon is excluded from the calculations (Table 3) (see Discussion). Analysis of pairwise comparisons between individual ITS sequences pointed to *Cutandia maritima* as the fastest-evolving taxon of the FEVRE clade for this genomic region; differences to rates shown by other taxa were significant in all cases except for the *Festuca rothmaleri*, *Vulpia fontqueriana*, and *V. membranacea* ones (results not shown).

The % G + C content and the free energy of folding of the ITS1 region showed some differences among the studied taxa. The average percentage of guanine and cytosine residues was 60.5% for the ingroup taxa; however, slightly lower values were observed for the annual taxa (from 56.8% in *Vulpia membranacea* to 58.7% in *V. alopecuros*) than in the perennial ones (from 60.4% in *Festuca rivularis* to 64.8% in *F. quadriflora*). *Cutandia maritima* showed the lowest content of G + C (54%), though this percentage is similar to that of other variable ingroup and outgroup annual species (i.e., *Poa infirma*, 56.5%). The variable perennial taxon *Festuca rothmaleri* had a percentage of 59%, close to the perennial outgroups *F. pratensis* and *Lolium perenne* (58%). Average Minimum Free Energy (MFE) of folding of the ITS1 RNA transcripts was −87.60 kcal/mol (sd = ± 6.96 kcal/mol) for the ingroup taxa. Folding energies also showed slight

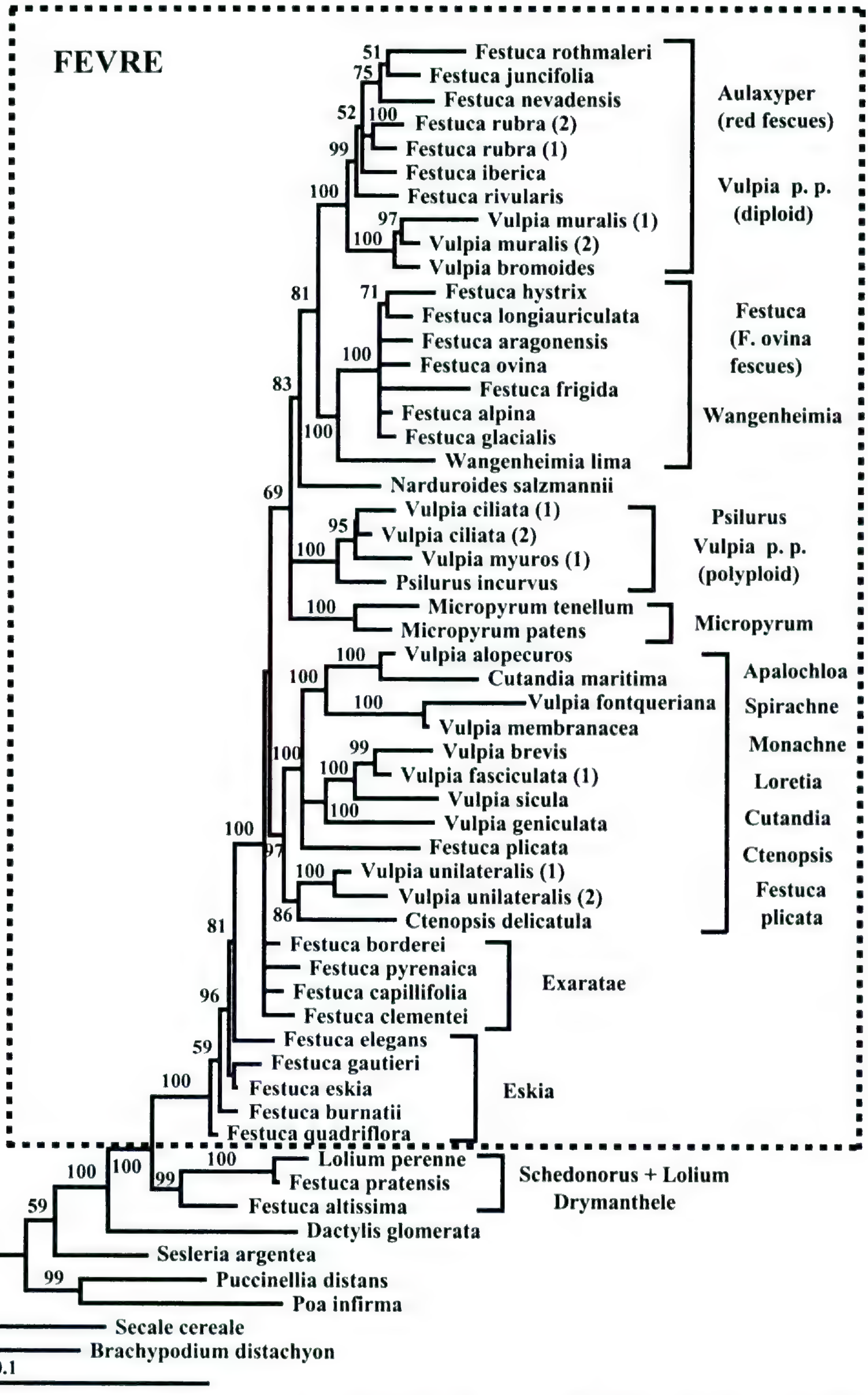

Figure 6. Combined ITS/*trn*L-F: Bayesian 50% MR consensus tree of 9643 trees. Posterior probability percentage is indicated on the corresponding branches. Species numbers correspond to different accessions of the same taxon (see Table 2).

Table 3. Relative Rate Test between lineages and groups of the FEVRE clade. *Festuca pratensis* was used as outgroup. dK = differences in rate substitutions between compared groups; sd-dK = standard deviation; P = probability value of the test (** significance at $P < 0.01$; * significance at $P < 0.05$); (a) = *Cutandia maritima* included; (b) = *Cutandia maritima* excluded. Species groups refer to classical taxonomic circumscriptions except for the *Exaratae* group (which also includes *F. clementei* and *F. pyrenaica*) and the *Loretia* group (which also includes *Spirachne* and *Monachne* representatives) (see Table 2).

		ITS			*trn*L-F		
Group 1	Group 2	dK	sd-dK	P	dK	sd-dK	P
Eskia	*Aulaxyper*	0.023149	0.008647	0.007432**	0.013429	0.004027	0.000859**
Eskia	*Festuca*	0.018063	0.006391	0.004714**	0.016959	0.004903	0.000546**
Eskia	*Exaratae* gr.	0.010546	0.005296	0.046484*	0.004773	0.002793	0.087474
Eskia	*Vulpia* (diploid)	0.032505	0.00884	0.000239**	0.012807	0.004524	0.004652**
Eskia	*Psilurus*+*Vulpia* (polyploid)	0.025822	0.007549	0.000629**	0.011595	0.003764	0.002073**
Eskia	*Loretia* gr. (a)	0.046645	0.007569	1.00E−07 (a)**	0.02061	0.003747	1.00E−07**
Eskia	*Loretia* gr. (b)	0.044558	0.007343	1.00E−07 (b)**			
Eskia	*Apalochloa*	0.034817	0.008509	4.45E+00**	0.009349	0.003829	0.014631*
Eskia	*Ctenopsis*	0.036967	0.009771	0.000158**	0.026096	0.006113	2.12E+00**
Eskia	*Micropyrum*	0.038769	0.009973	0.000104**	0.008125	0.004285	0.05794
Eskia	*Narduroides*	0.023979	0.00857	0.005146**	0.017191	0.005522	0.001856**
Eskia	*Wangenheimia*	0.037625	0.010154	0.000214**	0.013195	0.004948	0.007668**
Aulaxyper	*Festuca*	0.005972	0.009773	0.541173	−0.005207	0.004733	0.271247
Aulaxyper	*Exaratae* gr.	0.012444	0.007417	0.093406	0.008566	0.004067	0.035199*
Aulaxyper	*Vulpia* (diploid)	0.001683	0.008013	0.833629	−0.001428	0.002463	0.562023
Aulaxyper	*Psilurus*+*Vulpia* (polyploid)	−0.001718	0.010472	0.869716	0.00042	0.004454	0.924849
Aulaxyper	*Loretia* gr. (a)	−0.020293	0.009494	0.032563 (a)*	−0.006134	0.004591	0.181494
Aulaxyper	*Loretia* gr. (b)	0.014832	0.009455	0.116726			
Aulaxyper	*Apalochloa*	−0.006944	0.011039	0.529303	0.003282	0.004869	0.500294
Aulaxyper	*Ctenopsis*	−0.00248	0.011051	0.82245	−0.00864	0.006208	0.164003
Aulaxyper	*Micropyrum*	−0.003863	0.008944	0.665796	0.003554	0.004981	0.475459
Aulaxyper	*Narduroides*	−0.00248	0.011195	0.8247	−0.000411	0.005319	0.938452
Aulaxyper	*Wangenheimia*	0.009575	0.010704	0.37104	0.00096	0.004434	0.8254
Festuca	*Exaratae* gr.	0.007989	0.004994	0.10971	0.011688	0.005099	0.0219*
Festuca	*Vulpia* (diploid)	0.013518	0.009483	0.154018	−0.003857	0.005053	0.44531
Festuca	*Psilurus*+*Vulpia* (polyploid)	−0.015133	0.008789	0.085104	0.004223	0.005326	0.427864
Festuca	*Loretia* gr. (a)	−0.033312	0.007518	1.07E+00 (a)**	−0.003363	0.005497	0.540653
Festuca	*Loretia* gr. (b)	0.028894	0.007446	0.000107 (b)**			
Festuca	*Apalochloa*	−0.025112	0.009467	0.007996**	0.007393	0.005652	0.190819
Festuca	*Ctenopsis*	−0.015512	0.008894	0.081154	−0.002855	0.006737	0.671756

Table 3. Continued.

Group 1	Group 2	ITS			*trn*L-F		
		dK	sd-dK	P	dK	sd-dK	P
Festuca	*Micropyrum*	−0.028149	0.010659	0.008278**	0.00824	0.005749	0.151803
Festuca	*Narduroides*	−0.013167	0.009495	0.165525	−0.000458	0.006477	0.943622
Festuca	*Wangenheimia*	−0.023047	0.009989	0.021052*	0.003558	0.005132	0.488147
Exaratae gr.	*Vulpia* (diploid)	0.023422	0.008151	0.004066**	0.007194	0.004383	0.100725
Exaratae gr.	*Psilurus*+*Vulpia* (polyploid)	−0.016538	0.007794	0.033853*	−0.00647	0.003817	0.090026
Exaratae gr.	*Loretia* gr. (a)	−0.036142	0.006437	1,00E−07 (a)**	−0.015114	0.003209	5,81E−01**
Exaratae gr.	*Loretia* gr. (b)	0.034958	0.006334	1,00E−07 (b)**			
Exaratae gr.	*Apalochloa*	−0.026026	0.008348	0.001827**	−0.004807	0.003475	0.166599
Exaratae gr.	*Ctenopsis*	−0.023676	0.007919	0.002795**	−0.021615	0.006084	0.000385**
Exaratae gr.	*Micropyrum*	−0.029772	0.009476	0.001684**	−0.003371	0.004449	0.44875
Exaratae gr.	*Narduroides*	−0.013484	0.007499	0.072166	−0.01244	0.005539	0.024714*
Exaratae gr.	*Wangenheimia*	0.0282	0.009479	0.002937**	0.004862	0.004648	0.295619
Loretia gr. (a)	*Vulpia* (diploid)	−0.021551	0.010393	0.038126 (a)*	−0.00803	0.004848	0.097628
Loretia gr. (b)	*Vulpia* (diploid)	0.018055	0.009845	0.066692			
Loretia gr. (a)	*Psilurus*+*Vulpia* (polyploid)	0.01763	0.009357	0.05954	0.007968	0.004445	0.07309
Loretia gr. (b)	*Psilurus*+*Vulpia* (polyploid)	0.01739	0.008957	0.052214			
Loretia gr. (a)	*Apalochloa*	0.010115	0.009542	0.289141	0.01021	0.002967	0.000582**
Loretia gr. (b)	*Apalochloa*	0.009502	0.009131	0.298043			
Loretia gr. (a)	*Ctenopsis*	0.007509	0.010578	0.477778	−0.000436	0.004922	0.929426
Loretia gr. (b)	*Ctenopsis*	0.008307	0.009999	0.406141			
Loretia gr. (a)	*Micropyrum*	0.009237	0.010408	0.374841	0.012252	0.004318	0.004554**
Loretia gr. (b)	*Micropyrum*	−0.00157	0.010235	0.878051			
Loretia gr. (a)	*Narduroides*	0.019497	0.008741	0.02572 (a)*	0.006341	0.005403	0.240554
Loretia gr. (b)	*Narduroides*	0.012888	0.008564	0.132363			
Loretia gr. (a)	*Wangenheimia*	−0.012255	0.010847	0.258578	−0.010009	0.00482	0.037871*
Loretia gr. (b)	*Wangenheimia*	0.00393	0.010881	0.717964			
Vulpia (diploid)	*Psilurus*+*Vulpia* (polyploid)	0.001801	0.010073	0.858094	0.000301	0.004622	0.948043
Vulpia (diploid)	*Apalochloa*	−0.01115	0.011317	0.324476	0.002329	0.004975	0.639666
Vulpia (diploid)	*Ctenopsis*	0.000954	0.010716	0.929046	−0.012228	0.006936	0.07794
Vulpia (diploid)	*Micropyrum*	−0.015468	0.010641	0.146063	0.003575	0.005398	0.507791
Vulpia (diploid)	*Narduroides*	−0.000573	0.010491	0.956445	−0.004267	0.005943	0.47276
Vulpia (diploid)	*Wangenheimia*	−0.012141	0.012042	0.313349	−0.000322	0.005061	0.949196

Table 3. Continued.

Group 1	Group 2	ITS			*trn*L-F		
		dK	sd-dK	P	dK	sd-dK	P
Ctenopsis	*Psilurus*+*Vulpia* (polyploid)	0.008936	0.011353	0.431212	0.013773	0.006411	0.031688*
Ctenopsis	*Apalochloa*	0.001792	0.009788	0.854749	−0.016747	0.005912	0.004618**
Ctenopsis	*Micropyrum*	0.00621	0.012093	0.60759	0.017052	0.006618	0.009983**
Ctenopsis	*Narduroides*	0.012988	0.010522	0.217071	0.009095	0.007721	0.238803
Ctenopsis	*Wangenheimia*	0.009419	0.011648	0.418715	−0.011935	0.006277	0.057241
"fine-leaved" perennials	"fine-leaved" annuals	−0.025183	0.006659	0.000159**	−0.004996	0.00212	0.018459*
FEVRE perennials	*Eskia*	0.019636	0.006206	0.001562**	0.011087	0.002816	8.45E+00**
FEVRE annuals	*Eskia*	0.031168	0.005981	4.38E−03**	0.013218	0.002995	1.14E+00**
Core FEVRE perennials	Core FEVRE annuals	0.009279	0.005389	0.085072	−0.002331	0.002113	0.269934

differences between annual and perennial taxa though the spanning ranges overlapped across several taxa. The perennial lineages had in general more stable predicted structures (from −100.20 kcal/mol in *Festuca quadriflora* to −78.60 kcal/mol in *F. rubra*) than the annual ones (from −98.10 kcal/mol in *Wangenheimia lima* to −78.60 kcal/mol in *Micropyrum patens*). *Cutandia maritima* reflected the poorest folding dynamic (−70.50 kcal/mol) of all analyzed taxa though *Festuca frigida* and other outgroup taxa also showed high MFE values (*F. frigida* = −71.60 kcal/mol, *Dactylis glomerata* = −72.00 kcal/mol, *Poa infirma* = −73.4 kcal/mol).

Discussion

Circumscription of FEVRE, polyphyly of *Vulpia* and paraphyly of the fine-leaved *Festuca*

One of the main conclusions of this study is the confirmation that FEVRE is a complex group that includes not only all lineages of *Vulpia* and the four of fine-leaved *Festuca*, as considered herein, but also the annual genera *Psilurus*, *Wangenheimia*, *Ctenopsis*, *Micropyrum*, *Narduroides*, and *Cutandia*. This group is monophyletic and well supported and clearly differentiated from the "broad-leaved" *Festuca* and from other sampled Poeae that have been used here as outgroups (Figs. 5 and 6).

It is also relevant to have demonstrated that the genus *Vulpia*, as presently constituted, is a polyphyletic assemblage of at least four distinct lineages. Conversely to what has been found for *Lolium*—a monophyletic group of taxa likely derived from a *Festuca pratensis* ancestor (Charmet et al., 1997; Gaut et al., 2000; Torrecilla & Catalán, 2002)—the *Vulpia* taxa do not share a common ancestry but have had independent origins within the fine-leaved fescues.

Within *Festuca*, the paraphyly of the different fine-leaved lineages has been shown, most interestingly in respect to the separate placement of the subsection *Exaratae* taxa versus sections *Festuca* and *Aulaxyper* taxa. The two groups include species with both intravaginal and extravaginal (or mixed) innovation shoots although they fall in different clades of the tree.

The basal sections *Eskia* and *Pseudatropis*

Section *Eskia* is shown to be paraphyletic, the representatives constituting the earliest-diverging lineages of the FEVRE clade. This basal position of the group is concordant with the extremely low substitution rates accounted for by its members.

Festuca elegans, classified in the monotypic section *Pseudatropis* by Krivotulenko (1960), is shown to be the closest relative of the core FEVRE taxa (Figs. 5 and 6), a result that is also correlated with the higher substitution rates accumulated by this species in its ITS genome. All the five taxa are mostly endemic diploids of the western Mediterranean area. They have been classified in *Festuca* sect. *Eskia* Willk. p.p. (= sect. *Variae* ser. *Intravaginales* Hack.) because they share several plesiomorphic traits, such as pubescent ovary apices, broad scarious margins of glumes and lemma, and a caryopsis free from the palea.

The consecutive divergence of a resolved lineage of three species (*Festuca quadriflora* (*F. gautieri* + *F. eskia*)) followed by that of *F. burnatii* in the parsimony-based tree (Fig. 5) is partially contradicted in the consensus Bayesian tree where *F. quadriflora* and *F. burnatii* are resolved as the succesive oldest lineages of this group (Fig. 6), though none of these relationships is strongly supported. Both *F. quadriflora* and *F. gautieri* hybridize spontaneously with *F. eskia*, which indicates a close genetic relationship among them. Conversely, *F. burnatii*, an isolated endemic from northern Spain that differs morphologically from the other taxa, does not intercross with any other sympatric member of the Eskia group. *Festuca elegans* shares with the above taxa the overall morphological attributes, being a relatively tall fescue with thin scabrous leaves. Krivotulenko (1960) classified *F. elegans* in its own section *Pseudatropis* based on its glabrous ovary apex, orbicular to ovate hilum, and elliptic lemma; however, Torrecilla et al. (2003), in their recent morphological survey of *Festuca* sect. *Eskia* and related allies, demonstrated that the characters used by Krivotulenko were not stable across the geographical range of the species, rejecting the separate sectional treatment proposed by this author. The *trn*L-F data set indicates a close relationship of *F. elegans* with *F. gautieri* and *F. eskia* (Figs. 3 and 4), whereas the ITS data set supports the closeness of this taxon to the core group of FEVRE (Figs. 1 and 2). The combined ITS and *trn*L-F analysis provides the same sister relationship for *F. elegans* and the FEVRE core taxa with moderate bootstrap support. A larger taxon sampling of representatives of *Festuca* sect. *Eskia* and other close groups will be necessary in order to resolve the phylogeny of the basal lineages of the FEVRE clade.

VULPIA SECT. *VULPIA* P.P. (DIPLOIDS) AND *FESTUCA* SECT. *AULAXYPER*

One of the best resolved lineages of the tree is that of Aulaxyper + diploid Vulpia (Figs. 5 and 6), a clade that shows high bootstrap and posterior percentage support for most of its branches. Although the sampling of representatives of *Festuca* sect. *Aulaxyper* only covers a small percentage of the species attributed to this group (Ainscough et al., 1986) it includes the type species and some of the typical members of the *F. rubra* complex. The proximity of diploid *Vulpia* sect. *Vulpia* taxa (*V. muralis*, *V. bromoides*) to *Festuca* sect. *Aulaxyper* is strongly supported in the *trn*L-F based topology (Figs. 3 and 4) and less supported in the ITS based one (Figs. 1 and 2). The combined ITS and *trn*L-F data matrix recovers the same sister relationships as the separate data sets and reinforces the robustness of this clade. Phylogenetic analyses conducted exclusively with the diploid data sets recovered the same evolutionary links for *F. rivularis*, one of the few diploid representatives of the *Aulaxyper* group, and the two diploid *Vulpia* taxa studied in this survey (*V. bromoides*, *V. muralis*) (results not shown). This *Vulpia* annual lineage could have derived from *Aulaxyper* perennial ancestors from which it likely inherited its chloroplast genome. The substitution rates shown by the two groups were similar for both the ITS and the *trn*L-F regions, the *Aulaxyper* assemblage being the most rapidly evolving lineage of all perennial FEVRE groups. The close phylogenetic relationships found between representatives of the red fescues and of diploid representatives of *Vulpia* sect. *Vulpia* (Figs. 3–6) are partially in agreement with their assumed genetic relatedness corroborated by intergeneric spontaneous hybrids (Ainscough et al., 1986) but strongly contrast with all current classifications of *Vulpia* sect. *Vulpia* (Cotton & Stace, 1977; Stace, 1981), especially for the separate evolutionary placements of the respective diploid and polyploid lineages.

Within Aulaxyper an evolutionary trend from low to high ploidy level taxa ($2n = 2x$ to $6x$–$8x$–$10x$) and from slender to more robust plants could be suggested along the clades of the group when the polyploid species are superimposed on the diploid tree (Figs. 5 and 6). *Festuca rivularis* (diploid), a plant endemic to the mountains of southern Europe and Turkey, is resolved as sister to the other taxa in the ITS and combined trees (Figs. 1, 2, 5, 6) but collapses in a polytomy with other lineages in the chloroplast-based tree (Fig. 3). The remaining Aulaxyper lineages correspond to polyploid taxa of the *Festuca rubra* complex. Hexaploid representatives of this group collapse in a polytomy with a clade of high polyploids; these taxa include two grassland species, the typical Euro-Siberian *Festuca rubra*, and the western Mediterranean *Festuca iberica*. The high polyploidy clade is formed by the octoploids

Festuca juncifolia and *F. rothmaleri* and the decaploid *Festuca nevadensis*. These are robust taxa endemic to territories of western Europe and northern Africa. The octoploid taxon *F. rothmaleri* accounts for the highest nucleotide substitution rates found within the FEVRE perennials in both ITS and *trn*L-F sequences as reflected in its long branches in the Bayesian trees (Figs. 2 and 4). Optimal minimum folding energies and estimated structures of the RNA transcript are similar to those of other *Festuca* taxa. The elevated rates of variability detected in the ITS region of these perennial polyploids are in agreement with the findings of Gaut et al. (2000) who recorded higher levels of ITS diversity in several polyploid taxa of *Festuca* subg. *Schedonorus* and of *Festuca* sect. *Aulaxyper* than in their diploid relatives. The rapid rate of evolution shown by this perennial group of polyploid red fescues can be likely associated to their putative recent hybrid origin (Kerguélen & Plonka, 1989).

FESTUCA SECT. *FESTUCA* AND *WANGENHEIMIA*

Another circumscribed group of taxa of the combined ITS and *trn*L-F trees is that corresponding to the Festuca group, which shows total bootstrap support (Fig. 5). This clade is recovered in the two separate ITS and *trn*L-F analyses with relatively high bootstrap and posterior probability support, but the relationships among the taxa are unresolved in most cases (Figs. 1–4). Similar lack of resolution is observed in the consensus tree depicted in Figure 5 except for the sister relationship of *Festuca frigida* to the remaining taxa. The Festuca lineage shows an intermediate rate of nucleotide substitution among the perennial FEVRE groups, which is lower if compared to those of the annual ones. However, *F. frigida* (diploid), a tiny restricted endemic plant from Sierra Nevada (southern Spain), presents the highest mutation rates within the studied "ovina" fescues. The higher substitution rate of this taxon might be reflected in its sister placement in the ITS and combined trees (Figs. 1, 2, 5, 6). Inclusion of *F. aragonensis* (tetraploid) and *F. indigesta* (hexaploid), the only polyploid representatives of this group sampled in the study, in the analyses did not alter the topologies of the diploid-based trees (results not shown). The relationships between these polyploid species with respect to their potential diploid relatives could not be established firmly due to the overall lack of resolution of the clade and to the present shortage in taxon sampling for this largest group of predominantly holarctic *Festuca* taxa (Ainscough et al., 1986). However, some insights about taxonomic and biogeographical relationships among the studied taxa could be speculated on from the clades recovered in the chloroplast *trn*L-F tree (Figs. 3, 4). The Festuca clade shows a polytomy of the Euro-Siberian-boreal terminal taxon *Festuca ovina* (diploid), an unresolved western Mediterranean mountain clade formed by *F. frigida* and the close vicariant diploid taxa *F. alpina* and *F. glacialis*, and a polytomic clade of Mediterranean steppe orophytes *Festuca hystrix* (diploid) and three members of the *F. indigesta* complex (Saint-Yves, 1925; Markgraf-Dannenberg, 1985), hexaploid *F. indigesta* and the sister taxa *F. longiauriculata* (diploid) + *F. aragonensis* (tetraploid). Two other studied taxa that have been conventionally classified within the *Festuca* section (*F. plicata* and *F. clementei*) (Markgraf-Dannenberg, 1980; Fuente & Ortuñez, 1998) fall apart from this clade. Both species bear distinctive morphological traits that separate them from the typical "ovina" fescues and show substantial differences in their respective substitution rates. The odd resolution of these *Festuca* taxa may indicate that the broad *Festuca* sect. *Festuca* taxon, as presently circumscribed, may be an artificial assemblage of different lineages in need of deeper investigation. Our resolved *Festuca* lineage includes the type species and other consectional taxa that share most of the distinctive morphological traits of the "ovina" group.

Wangenheimia is resolved as sister to the Festuca clade in the combined ITS and *trn*L-F trees (Figs. 5 and 6) and in the separate *trn*L-F topologies (Figs. 3 and 4), both with relatively high bootstrap and posterior percentage support. However, this taxon is linked to *Vulpia unilateralis* in the ITS-based trees (Figs. 1 and 2). Substitution rates of *Wangenheimia* are similar to those of the other annual lineages but higher than the *Festuca* ones. However, *Wangenheimia* shares with the "ovina" group several nucleotide synapomorphies and a 5 bp indel in the *trn*L-F region; exclusion of this gap character did not alter the topology of the clade, which also showed relatively high support indicating that *Wangenheimia* could have acquired its chloroplast genome from an ancestral *Festuca* donor. *Wangenheimia* shows few morphological affinities with the *Festuca* taxa but more with the *Vulpia* ones. However, *Wangenheimia* is distinguished from *Vulpia* and resembles *Festuca* sect. *Festuca* in its two subequal glumes and unawned lemmas. This taxon is distributed in xeric continental areas of the western Mediterranean region.

VULPIA SECT. *VULPIA* P.P. (POLYPLOID) AND *PSILURUS*

The clade Psilurus + polyploid Vulpia (*Vulpia* sect. *Vulpia* p.p.) shows one of the highest bootstrap values within the core FEVRE groups (Fig. 5). The common ancestry of tetraploids *Psilurus incurvus* and *Vulpia ciliata* and hexaploid *Vulpia myuros* is recovered in both the ITS tree (Fig. 1) and the *trn*L-F tree (Fig. 3), though the phylogenetic relationships of this polyploid lineage to other potential FEVRE relatives have not been yet resolved. The Bayesian 50% majority-rule consensus tree shows the Psilurus + polyploid Vulpia group nested in an unresolved clade that also includes the Aulaxyper + diploid Vulpia lineage and their allies in a separate subclade (Fig. 6). The expected close relatedness of the polyploid *Vulpia* sect. *Vulpia* taxa to the other consectional diploid taxa (Cotton & Stace, 1977; Stace, 1981) has not been confirmed by the present data. Representatives of the two polyploid species intermix in a clade sister to *Psilurus* in the ITS and ITS/*trn*L-F based trees (Figs. 1, 2, 5, 6), though they collapse with *Psilurus* in a polytomy in the *trn*L-F based trees (Figs. 3, 4). The close relatedness of *Vulpia ciliata* and *Vulpia myuros* is mostly based on the ITS characters (Figs. 1, 2). Substitution rates of the Psilurus + polyploid Vulpia lineage are roughly similar to those of the diploid *Vulpia* lineage for both ITS and *trn*L-F sequences; however, the two groups show the lowest substitution rates of all *Vulpia* taxa indicating a likely slower evolutionary pace. Differences are especially noticeable with respect to the highly heterogeneous sequences of the *Loretia* assemblage.

The relatedness of *Vulpia ciliata* and *V. myuros* is congruent with some of their shared morphological attributes, otherwise characteristic of the typical section *Vulpia* (Cotton & Stace, 1977); however, the link of these two taxa to *Psilurus* is more unexpected. Hexaploid *Vulpia myuros* is the type species of the genus; this taxon strongly resembles diploids *Vulpis muralis* and *V. bromoides* in gross morphology, although our molecular data do not support a close phylogenetic relationship. *Vulpia ciliata* and *Psilurus* share a 3-veined lemma, a 1-veined upper glume, and swollen epidermal cells. *Vulpia ciliata* bears other unusual traits that are not present in typical section *Vulpia*, such as spikelets with large distal sterile florets and a hyaline margin of the upper glume (Paunero, 1964; Cotton & Stace, 1977). *Psilurus* has been considered to be close to section *Apalochloa* in *Vulpia* (*V. unilateralis*) based on several morphological and anatomical characters (Vignal, 1979); however, placement of the latter taxon is rather ambiguous (Figs. 1–4).

VULPIA SECTS. *SPIRACHNE, MONACHNE, LORETIA,* AND *APALOCHLOA, CUTANDIA, FESTUCA PLICATA,* AND *CTENOPSIS*

A monophyletic group resolved by the combined ITS and *trn*L-F analysis is that of the sections *Spirachne*, *Monachne*, *Loretia*, and *Apalochloa* of *Vulpia* plus *Cutandia maritima*, *Festuca plicata*, and *Ctenopsis delicatula* (Figs. 5 and 6). Representatives of three sections of *Vulpia* (sects. *Spirachne*, *Monachne*, *Loretia*), *Cutandia maritima*, and *Festuca plicata* are distinctly resolved in a moderately supported clade, whereas those of *Vulpia* sect. *Apalochloa* and *Ctenopsis* link in a clade sister to the former clade though none of these relationships is supported (Fig. 5). The monophyly of the first group is mostly based on ITS data (Figs. 1, 2), whereas the link of these two lineages with those of representatives of *Festuca* sect. *Exaratae* plus *F. pyrenaica* and *F. clementei* is recovered by the *trn*L-F characters (Fig. 3). Deletion of one 4 bp *trn*L-F indel from the analysis provokes the disarticulation of this group, except for the two single subclades supported by nucleotide characters in the parsimony-based tree (Fig. 3); nonetheless, the monophyly of the Spirachne + Monachne + Loretia + Cutandia + F. plicata assemblage is recovered with relative high support in the Bayesian tree (Fig. 4), which is only based on sequence data.

Sections *Monachne* and *Loretia* intermix in the two separate subclades recovered by the ITS data (Figs. 1, 2) and in the combined trees (Figs. 5, 6). *Vulpia brevis*, the single taxon of section *Spirachne*, is resolved as the closest relative of *Vulpia fasciculata*, the type species of section *Monachne* (Figs. 5, 6), a relationship mostly based on the ITS characters (Figs. 1, 2). The two sister taxa (Vulpia brevis + V. fasciculata) share a number of structural characters, like a cleistogamous breeding system, spikelets with an apical group of sterile florets, awned upper glume, and distally dilated pedicels, that were postulated by Cotton and Stace (1977) as evidences of their close taxonomic relatedness. *Vulpia sicula* is the next closest relative of the Vulpia brevis + V. fasciculata pair (Figs. 1, 2, 5, 6). The taxon shows a chasmogamous breeding system and full fertile flowered spikelets, characters that are typical of *Vulpia* sect. *Loretia*; most noticeably, *Vulpia sicula* is a perennial caespitose species that can hybridize with *Festuca rubra* in experimental crosses though not spontaneously (Barker & Stace, 1982). Based on morphological, karyological, and reproductive characters Stace and Cotton (1973) considered *Vulpia sicula* to be related to other *Vulpia* sect. *Loretia* taxa. Our ITS data indicate that *Vulpia si-*

cula is most likely a close relative of *Vulpia* species of sections *Spirachne*, *Monachne* (*V. fasciculata* herein), and *Loretia* (*V. geniculata* herein) (Figs. 1, 2, 5, 6) though the cpDNA data point toward some unsupported affinity of *V. sicula* to *V. unilateralis* (Figs. 3 and 4). *Vulpia geniculata*, another representative of section *Loretia* that bears large reproductive organs, is also nested in this clade and resolved as sister to the previous group.

The resolution of the second group of *Vulpia* taxa ((Vulpia membranacea + V. fontqueriana), (Vulpia alopecuros + Cutandia)) is highly supported in both the combined and the ITS-based topologies (Figs. 1, 2, 5, 6); the sister relationships of *Vulpia alopecuros* and *Cutandia maritima* are also recovered in the *trn*L-F tree (Figs. 3, 4). *Vulpia membranacea* and *V. fontqueriana* are very similar morphologically; *V. fontqueriana* was described from southern Spain by Melderis and Stace (1968) based on its single fertile floret per spikelet and long pointed lemma callus. These two diploid representatives of *Vulpia* sect. *Monachne* show the typical characters of this group (cleistogamous breeding system, reduced number of fertile flowers per spikelet), but they do not link together with the type species (*V. fasciculata*) in the ITS-based tree (Figs. 1, 2). Inclusion of tetraploid *V. fasciculata* in the diploid data set analysis resolved it as sister to diploid *V. brevis* but not to their consectional taxa. By contrast, the Bayesian *trn*L-F analysis resolves *V. fasciculata* as sister to a consectional low-supported V. membranacea + V. fontqueriana clade and links *V. brevis* to the V. alopecuros + Cutandia maritima clade (Fig. 4). Because all representatives of *Vulpia* sects. *Monachne* and *Spirachne* (monotypic) have been sampled in the present study, the monophyly of section *Monachne* is disputed by the more abundant ITS characters (Figs. 1, 2, 5, 6) but not by the *trn*L-F ones (Fig. 4). The tetraploid taxon *V. fasciculata* is likely of hybrid origin (*Monachne* × *Spirachne*), having inherited its chloroplast genome from a *Monachne* ancestor. The resolved patterns are in general agreement with classical circumscriptions of these groups and have provided an evolutionary framework to explain the origin of tetraploid *V. fasciculata*.

Resolution of the clade V. alopecuros + Cutandia maritima is recovered by both ITS and *trn*L-F data with high bootstrap and posterior probability support (Figs. 1–4) and is therefore reflected in the combined trees (Figs. 5, 6). However, the close relatedness shown by *Cutandia maritima* to this *Vulpia* group is mostly unexpected. Stace (1978b) suggested a close taxonomic affinity of *Cutandia* to *Desmazeria*, whereas Soreng and Davis (2000) found *Cutandia* (*C. memphytica*) to be nested within their "Parapholiinae" clade in a grade of Sphenopus (Cutandia (Catapodium (Desmazeria (Hainardia + Parapholis)))). The sister relationship of *Cutandia maritima* to *V. alopecuros* is based on several synapomorphic ITS and *trn*L-F nucleotide characters being the only group of the clade that is not disassembled when the *trn*L-F indels are excluded from analysis (results not shown). The extremely high substitution rate showed by *C. maritima* in its ITS region, reflected by the length of its branch in the Bayesian-based tree (Fig. 2), was correlated with its low % G + C content and the high minimum-free folding energies of its ITS1 RNA transcript, though those values were not dramatically different from the ones estimated for other ingroup and outgroup taxa. These results suggest that the ITS sequence of *C. maritima* could be a putative pseudogene or just a highly variable one. The distorting effects caused by paralogous ITS copies in phylogenetic reconstruction have been manifested in different analyses of angiosperms (Buckler et al., 1997; Mayol & Rosselló, 2001). Phylogenies potentially affected by ITS pseudogenes have also been reported in *Lolium* (Gaut et al., 2000). In order to avoid the risk of recovering a spurious phylogeny, the ITS analyses were reconducted deleting *Cutandia maritima* from the data set. The parsimony and Bayesian trees showed the same topology and similar levels of branch support to the ones depicted in Figures 1 and 2 (results not shown), indicating that the exclusion of this species does not alter the relationships recovered for the remaining taxa. Even leaving out the information provided by the ITS data, the *trn*L-F data still recover a sister relationship for *V. alopecuros* and *C. maritima*, the only well-supported clade of this group (Figs. 3, 4). *Cutandia maritima* shows an intermediate rate of substitution in this chloroplast genome region, not significantly higher than that of *V. alopecuros* and similar to those of other *Vulpia* sect. *Loretia* taxa (results not shown). Therefore, the relationships presented here between *C. maritima* and *V. alopecuros* are strongly supported by *trn*L-F data. A larger sampling of representatives of *Cutandia* will be necessary in order to establish its phylogenetic relationships within the festucoids and other related lineages and to determine if this taxon is a natural genus. The placement of *Vulpia alopecuros* in the clade is congruent with its taxonomic affinities; this taxon bears the general attributes of section *Loretia* but presents a glabrous ovary apex, pointed elongated callus, and a minute 1-veined lower glume (Cotton & Stace, 1977). Barker and Stace (1984, 1986) indicated the ex-

treme genetic isolation of *Vulpia alopecuros* from other *Vulpia* taxa and suggested a distinct sectional treatment for it. Our results resolve *V. alopecuros* as the sister taxon of the V. membranacea + V. fontqueriana clade.

Festuca plicata, a taxon classified within *Festuca* sect. *Festuca*, shows an unexpected relatedness to this Spirachne + Monachne + Loretia + Cutandia group (Figs. 5, 6) that is confirmed by the two separate ITS and *trn*L-F based analyses (Figs. 1–4). Diploid *Festuca plicata* is an endemic Ibero-Mahgrebian taxon characterized by several uncommon *Festuca ovina* traits; it resembles *Vulpia* in its long-awned lemma. *Festuca plicata* was recently included in *Festuca* sect. *Festuca* by Fuente and Ortuñez (1998); our combined ITS and *trn*L-F analysis demonstrates that *Festuca plicata* is not related to the studied "ovina" group but to this clade of *Vulpia* taxa.

Vulpia unilateralis, the single representative of *Vulpia* sect. *Apalochloa* is recovered as the sister taxon of *Ctenopsis* in the combined trees depicted in Figures 5 and 6; however, its phylogenetic placement is not satisfactorily resolved in any of the independent ITS and *trn*L-F analyses (Figs. 1–4). *Vulpia unilateralis* is shown to be related to *Wangenheimia*, *Narduroides*, and *Ctenopsis* in the ITS Bayesian tree (Fig. 2) but is nested within the Spirachne + Monachne + Loretia clade in the *trn*L-F Bayesian tree (Fig. 4), though none of those relationships is well supported. The distinctness of section *Apalochloa* from other sections of the genus *Vulpia* is corroborated by several characters; *Vulpia unilateralis* bears a single-borne spikelet per node, shortly awned lemma, and several anatomical patterns in vegetative and floral epidermises that link it to *Psilurus* (Vignal, 1979). Despite the apparent similarities between these two taxa, our results indicate that *Vulpia unilateralis* and *Psilurus incurvus* belong to different phylogenetic lineages of the FEVRE group.

Ctenopsis delicatula is a close relative of this Spirachne + Monachne + Loretia + Cutandia + Festuca plicata group. This annual taxon shows a sister relationship to *Vulpia geniculata* in the *trn*L-F Bayesian tree (Fig. 4) but is otherwise unresolved within the FEVRE clade in the ITS parsimony based topology (Fig. 1). The combined ITS and *trn*L-F analysis recovers a sister relationship of *Ctenopsis delicatula* to *Vulpia unilateralis* favored by the ITS characters. *Ctenopsis* has been frequently classified within *Vulpia* based on their strongly unequal glumes and some other floral traits (Clayton & Renvoize, 1986) but is distinguished from it by its rigid panicle, and a caryopsis free from the palea with a short hilum (Paunero, 1963; Cotton & Stace, 1977).

Representatives of the four sections *Monachne*, *Spirachne*, *Loretia*, and *Apalochloa* of *Vulpia* form a distinct though paraphyletic assemblage within the FEVRE group; *Cutandia maritima*, *Festuca plicata*, and *Ctenopsis delicatula* are nested within it. This group shows the highest substitution rates of all studied FEVRE lineages for both genomes, though they are more pronounced in the ITS region (even when *C. maritima* is excluded from analyses), thus raising contention about the loss of deep phylogenetic signal in the highly heterogeneous taxa and the potential influences that long-branch attraction and site saturation might have inflicted on these phylogenies. Despite the potential risk of some artifactual relationships caused by an excess of homoplasy, the evolutionary framework depicted here shows a close relationship for most of the *Vulpia* lineages, which likely form a paraphyletic group recently derived from a common ancestor. On the other hand, the separate placements shown by representatives of the typical *Vulpia* sect. *Vulpia* clearly demonstrate the polyphyly of this genus.

FESTUCA SUBSECT. *EXARATAE*, *F. CLEMENTEI*, *F. PYRENAICA*

Some unresolved taxa of the core FEVRE group are those belonging to *Festuca* subsect. *Exaratae* (*Festuca borderei*, *F. capillifolia*) plus *Festuca clementei* and *F. pyrenaica*. These taxa form a paraphyletic basal lineage to the Spirachne + Monachne + Loretia + Apalochloa + Cutandia + F. plicata + Ctenopsis clade in the combined parsimony-based ITS and *trn*L-F tree (Fig. 5) where the four of them collapse in a polytomy with the clade of *Vulpia* taxa and its allies. This topological position is mostly coincident with that of the *trn*L-F parsimony-based tree (Fig. 3), though neither it nor the one in Figure 5 is supported. The link between these four taxa and the *Vulpia* clade is based in one *trn*L-F 4 bp indel; the Bayesian analysis, which includes only nucleotide characters, shows a basal unresolved position of this *Exaratae* group of taxa with respect to the more recently evolved FEVRE lineages in the *trn*L-F and combined trees (Figs. 4 and 6).

The *Exaratae* group was first circumscribed based on the possession of invaginate leaf sheaths (Saint-Yves, 1922); this taxon includes a variety with intravaginal versus extravaginal and intravaginal shoots (Saint-Yves, 1922; Maire, 1955; Markgraf-Dannenberg, 1985) that otherwise link them, respectively, to the *Festuca* and *Aulaxyper* groups

to which they have been frequently misattributed. Our two studied representatives of *Festuca* subsect. *Exaratae* and the *F. clementei* and *F. pyrenaica* taxa are narrow endemics of the western Mediterranean area, and each of them shows singular morphological traits. However, none is closely related to the core group of fine-leaved fescues, as demonstrated in the ITS and *trn*L-F based topologies (Figs. 5, 6). The basal position recovered for these lineages in the Bayesian trees is in agreement with the low substitution rates detected in their chloroplast genome, which are significantly slower than those of the *Aulaxyper, Festuca,* and the annuals groups. Our preliminary results indicate that *Exaratae* s.l. (incl. *Festuca clementei* and *F. pyrenaica*) could represent older evolutionary lineages than those of the *Festuca ovina* and the *F. rubra* s.l. groups.

NARDUROIDES AND *MICROPYRUM*

An additional problem is manifested by the contrary placement of the genera *Micropyrum* and *Narduroides* that distantly attach to different lineages of the FEVRE clade on nuclear- and chloroplast-based reconstructions (Figs. 1–4). *Narduroides* is more closely related to *Apalochloa, Wangenheimia,* and *Ctenopsis* in the Bayesian ITS based tree (Fig. 2) but is sister to the *F. ovina* and *F. rubra* clade in both parsimony and Bayesian *trn*L-F based trees (Figs. 3, 4). Conversely, the *Micropyrum* clade is unexpectly resolved as sister to the *F. rubra* group in the ITS based trees (Figs. 1, 2) but as sister to the Psilurus + polyploid Vulpia clade in the *trn*L-F based trees (Figs. 3, 4). However, none of these relationships is well supported in any case. The two *Micropyrum* taxa included in this study (*Micropyrum tenellum, M. patens*) link together in highly supported generic clades (Figs. 1–4). The substitution rates shown by the *Micropyrum* and *Narduroides* lineages are similar to those found for the other ephemeral taxa except for the low rate of the *Narduroides* ITS region. This suggests that the distinct phylogenetic relationships recovered for each lineage might be influenced by different homoplasious changes. Alternatively, *Micropyrum* and *Narduroides* could be genera of hybrid origin with differently inherited genomes from their respective ancestors. None of these hypotheses can be resolved with the present data. *Narduroides,* a monotypic genus characterized by its subequal glumes, chartaceous to coriaceous lemmas, and a caryopsis slightly adherent to palea, with a punctiform hilum (Stace, 1978a) was considered to be related to the *Vulpia–Desmazeria* complex by Stace (1981) but was classified within tribe Hainardieae by Clayton and Renvoize (1986). Our phylogenetic results indicate that *Narduroides* may be a recently evolved taxon of the core FEVRE clade.

SUMMARY. HYBRIDIZATION, POLYPLOIDY, AND LIFE-CYCLE STRATEGIES AS THE MAIN DRIVING FORCES IN THE EVOLUTIONARY HISTORY OF THE FEVRE LINEAGES

The phylogenetic hypothesis recovered from the present study supports the four resolved lineages Aulaxyper + diploid Vulpia, Festuca + Wangenheimia, Psilurus + polyploid Vulpia, and Spirachne + Monachne + Loretia + Apalochloa + Cutandia + F. plicata + Ctenopsis within the FEVRE group after the separate and simultaneous analysis of the nuclear ITS and the chloroplast *trn*L-F regions. The first three lineages and two clades of the last group (Spirachne + V. fasciculata + Loretia and V. membranacea + V. fontqueriana + V. alopecuros + Cutandia) show strong to moderate bootstrap and posterior probabilities supports. A likely hypothesis of evolution for most of the studied taxa is presented in the trees depicted in Figures 5 and 6. Nonetheless, the phylogenetic relationships among these main groups still remain obscure; internal resolution of the deep branches of the FEVRE group has not been achieved with the present data set indicating that the failure of the sequenced regions to resolve the early divergences of this group of grasses could be associated with events related to lineage sorting, hybridization, and polyploidization, recurrent phenomena which are otherwise common in the grass family (Kellogg et al., 1996; Davis & Soreng, 1993; Soreng & Davis, 2000). The strong differences observed in the substitution rates among different lineages could also increase instances of homoplasy for the rapidly evolving taxa and might affect phylogenetic analysis with undesirable effects like long-branch attraction and site saturation (Hillis, 1998; Wendel & Doyle, 1998; Gaut, 1998). Despite potential cases of artifactual reconstruction for some rapidly evolving FEVRE groups, the concurrent phylogenetic resolution and the similar rates of substitutions obtained for the main FEVRE lineages indicate that the recovered topologies likely reflect their true evolutionary relationships.

Compelling evidences have demonstrated the key role played by hybridization in the speciation of the pooid grasses where both intergeneric and intrageneric taxa have been documented for several tribal lineages (Soreng & Davis, 2000, and references therein). Recurrent hybridization followed by polyploidy is a common phenomenon within the "fine-leaved" *Festuca* as demonstrated for most of

the *Festuca* sect. *Aulaxyper* taxa, which are considered hybrid-swarms of putatively recent origin (Ainscough et al., 1986). Introgressive hybridization and polyploidization constitute major driving evolutionary forces within the angiosperms (Stebbins, 1950, 1956; Brochmann et al., 1992; Soltis et al., 1995; Cook et al., 1998; Soltis & Soltis, 1999) where recurrent origins of polyploid species seem to be the rule rather than the exception. However, while multiple origins of recently formed polyploid taxa could be traced with confidence using appropriate molecular markers (Soltis et al., 1995; Cook et al., 1998), appalling conflicts arise in the resolution of old reticulation events where parental lineages may have become extinct or where hybrid derivatives show closer morphological and genomic affinities to one of the parental taxa. Well-documented cases have been presented for most intergeneric × *Festulpia* taxa that have gained the morphological attributes of the red fescue parent, which performed successfully as the pollen donor, showing their ability for repeated backcrossing with that parent but not with the female *Vulpia* one (Barker & Stace, 1984; Ainscough et al., 1986). Artificial crosses and derivative backcrosses that mirror the spontaneous hybridizations followed by these plants in the wild are clear examples of the difficulties of tracing back the identity of the original parental lineages in this highly introgressed FEVRE group.

Efforts to unravel the reticulation events postulated in this group of grasses have failed for some diploid lineages (i.e., *Narduroides*, *Micropyrum*) as well as for the polyploid Psilurus + Vulpia clade. Conflicting topologies from differently inherited genomes have been reported in the tribe Triticeae (Kellogg et al., 1996; Mason-Gamer & Kellogg, 1997), where organellar and nuclear data sets recover different histories of diploid genomes. Chloroplast-based phylogenies have been considered a safer way to recover the underlying evolutionary trends of highly reticulate groups, like in the Pooideae (Soreng & Davis, 2000), potentially avoiding the risks presented by recombinant nuclear characters and by admixed polyploid genomes. However, plastid data have led to incorrect pictures of evolutionary history in some angiosperm groups where more rapidly evolving nuclear genes have satisfactorily recovered the relationships at the deep internal branches of the trees (Cronn et al., 2002). In the FEVRE group, the more highly variable ITS region has proven to be the source of major informativeness though it is mostly concordant with that retrieved from the chloroplast. Additive polymorphisms, changes in concerted evolution of the ITS region toward one of the parental ribotypes, and recombinations may have also occurred in different lineages of the FEVRE group as these mechanisms operate in highly reticulate groups (Fuertes-Aguilar et al., 1999; Whitall et al., 2000). Such events could pass unobserved or be untraceable in extant organisms of recurrently introgressed groups, thus making more difficult the reconstruction of the past history of some lineages.

Ongoing in situ hybridization between different *Vulpia* species and the red fescues (*F. rubra* group) has been reported for representatives of *Vulpia* sect. *Vulpia* (*Vulpia myuros*, *V. bromoides*) and *Festuca* sect. *Aulaxyper* (*Festuca rubra*, *F. nigrescens*) (Ainscough et al., 1986) and of *Vulpia* sect. *Monachne* (*Vulpia fasciculata*) and *Festuca* sect. *Aulaxyper* (*Festuca rubra*, *F. juncifolia*) (Stace & Cotton, 1974). These spontaneous crosses have been interpreted as indicators of the close genetic relationships between the respective parental groups (Ainscough et al., 1986). The genetic affinities claimed for them are in close though not complete agreement with our phylogenetic results. The close relationship recovered for the diploid representative of *Vulpia* sect. *Vulpia* (*Vulpia bromoides*) and *Festuca rubra* is in contrast with the lack of apparent evolutionary links between polyploid representatives of *Vulpia* sect. *Vulpia* (hexaploid *Vulpia myuros*) and of section *Monachne* (tetraploid *Vulpia fasciculata*), which intercross more frequently with hexaploid and octoploid taxa of the *Festuca rubra* complex in the wild. These contradictions also extend to the disparate placements found for the diploid and polyploid *Vulpia* sect. *Vulpia* lineages within the FEVRE group. Assortative matching and recurrent polyploid formation, common phenomena in several groups of angiosperms (Soltis & Soltis, 1993), could have been the hidden mechanisms behind the multiple origins of these diverging *Vulpia* polyploids. Recently derived polyploid taxa, like those of the Psilurus + polyploid Vulpia clade, might have arisen at different evolutionary times. Although the identity of their potential genome donors has not been established yet, the close genomic affinities shown to the red fescues in present spontaneous intergeneric crosses and the morphological similarity of some of them (tetraploid and hexaploid *Vulpia* taxa) to consectional diploid taxa points toward the contribution of the Aulaxyper + diploid Vulpia lineage in their origin.

Substitution rates might also be indicative of different selection mechanisms that operate in the speciation process (Gaut et al., 1996; Barraclough et al., 1996; Barraclough & Savolainen, 2001; Jobson & Albert, 2002; Zhong et al., 2002). Relative rate tests conducted within the FEVRE group have

detected a general evolutionary pattern where old perennial lineages evolve significantly slower than the recently derived annual ones, suggesting the presence of some stabilizing selection acting on the perennial taxa in contrast to a rapid adaptive speciation of the ephemeral taxa. The multiple arrays of morphological and reproductive traits manifested by the FEVRE ephemeral taxa that moved taxonomists to classify them in different genera can be interpreted as the consequence of selection release resulting in rapid, pulse-like diversification events. In this respect, our findings support the speciation rate hypothesis that connects increased nucleotide substitution with increased taxonomic diversification (Barraclough et al., 1996; Barraclough & Savolainen, 2001). Although the acquisition of the annual life-cycle habit has presumably fostered the speciation rate of the ephemeral FEVRE taxa, other perennial lineages with relatively high rates of nucleotide substitutions but longer generation times (i.e., *Festuca* sect. *Aulaxyper*) may have also experienced an increased rate of cladogenesis. Torrecilla et al. (2003, and unpublished data) have recently found that some Macaronesian and American *Festuca* taxa currently attributed to different groups of the "broad-leaved" fescues (i.e., sect. *Amphigenes*, sect. *Subulatae*) are close relatives of the red fescues. The higher mutation rates shown by the *Aulaxyper* taxa compared to those of the other perennials might have resulted from diverse recurrent introgressions with other festucoid lineages increasing the genetic pool of this hybrid complex.

An evident evolutionary trend toward a short annual life-cycle and a reduction in habit and reproductive size has probably evolved several times within the FEVRE group as manifested in the Spirachne + Monachne + Loretia + Apalochloa + Cutandia + F. plicata + Ctenopsis lineage. By contrast, a progressive increase in size and robustness has been developed in the more recently evolved perennial complexes of the *F. rubra* group that are mostly formed by vigorous hybrid taxa that also propagate vegetatively. These apparently opposite life cycle and reproductive strategies coupled in each case with recurrent hybridization and polyploidy have been major factors that likely triggered the speciation processes within the separate lineages of the FEVRE group at different evolutionary times. The effects of selection processes focused on large mosaics of populations covering rapidly expanding broad geographic ranges after the glaciations, like those experienced by the successful polyploid and clonally propagating red fescues, must differ from those experienced by narrow endemic relictual species, like most of the annual and some of the oldest perennial FEVRE lineages. The evolutionary scenarios depicted here for the ephemeral and highly introgressed perennial lineages of the fine-leaved *Festuca* should be examined across other festucoid lineages where evolutionary trends toward short-life cycle or perennial polyploid-vigor have evolved independently in several lineages. Biogeographical patterns of most of the ephemeral FEVRE groups covered in the present survey indicate that these annual lineages likely radiated in the Mediterranean region, the area in which the potential diploid ancestors are endemics. An evolutionary hypothesis about an early divergence of most of the FEVRE diploid annual lineages (*Vulpia* sect. *Vulpia* p.p., *Micropyrum*, *Narduroides*, *Wangenheimia*) and of a secondary radiation of the highly polyploid complexes (*Festuca* sects. *Aulaxyper* and *Festuca* p.p.) are also supported by our phylogenies. A larger and more resolved framework should be constructed for the FEVRE lineages in order to estimate the date of speciation of these grasses.

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GEOGRAPHICAL DIVERSIFICATION OF TRIBES EPILOBIEAE, GONGYLOCARPEAE, AND ONAGREAE (ONAGRACEAE) IN NORTH AMERICA, BASED ON PARSIMONY ANALYSIS OF ENDEMICITY AND TRACK COMPATIBILITY ANALYSIS[1]

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Abstract

Tribes Epilobieae, Gongylocarpeae, and Onagreae, a monophyletic branch in the family Onagraceae, comprise genera endemic to or having their major basal radiation in the Madrean Floristic Region of southwestern North America. Parsimony analysis of endemicity (PAE) and panbiogeography (track compatibility analysis) were performed in order to seek an historical explanation for the patterns of high diversity and endemicity for the group in this region. Twenty-one areas of endemism are delimited, based on previous biogeographic schemes and presence of endemic plant and animal taxa. Based on distributional data on 173 species, a strict consensus PAE cladogram shows four main groups of areas: northern North America, the central Mexican areas, western North America, and eastern North America. Track compatibility analysis resulted in two strongly supported generalized tracks: one includes eastern North America, and the other western North America. PAE and panbiogeographical analyses of the distributional patterns of these taxa suggest a close relationship of eastern and western North America, with both areas more related to the Neotropics than to the Palearctic, and a rather weak association between northern North America and Asia. The discovery of two tracks in eastern and western North America for Epilobieae, Gongylocarpeae, and Onagreae reveal little relationship of North America with Asia or other continents. These tribes display a distinct but contemporaneous biogeographical history that differs from those of the Holarctic. These eastern and western tracks show that ancestral biotas existed on each side of North America, with the species of each track sharing a common history.

Key words: biogeography, endemicity, Madrean, Onagraceae, panbiogeography.

Recent developments in biogeography have highlighted the importance of the spatial distribution of organisms as a direct subject of analysis (Craw et al., 1999; Crisci, 2001; Crisci et al., 2000, 2003). The Onagraceae, a moderate-sized, sharply defined, homogeneous family, have been intensively studied (Raven, 1979, 1988; Hoch et al., 1993; Levin et al., 2003, 2004) and thus constitute an excellent group within which to develop such biogeographic studies.

The family Onagraceae includes six monogeneric tribes—Circaeeae, Fuchsieae, Gongylocarpeae, Hauyeae, Jussiaeeae, and Lopezieae—and two larger, more diverse tribes, Epilobieae and Onagreae (Raven, 1979; Hoch et al., 1993; Levin et al., 2003). Tribes Epilobieae, Gongylocarpeae, and Onagreae, which form a monophyletic branch in the family (Levin et al., 2003), are biogeographically distinct because almost all 11 genera in these tribes are endemic to or have had their major basal ra-

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diation in western North America. A primary concentration of genera exists in the Madrean Floristic Region (Takhtajan, 1986), comprising the southwestern United States and northern Mexico. This is an area of great geological and climatological complexity with a rich and highly characteristic biota (Axelrod, 1958; Axelrod & Raven, 1985; Takhtajan, 1986).

Gongylocarpus, until recently included in the Onagreae, and *Xylonagra* (Onagreae) are endemic to western North America, and *Camissonia*, *Clarkia*, and *Gayophytum* (all Onagreae) have the great majority of their taxa in the region, especially in the California Floristic Province (Raven & Axelrod, 1978); each of the latter three genera also has one or two species in temperate South America. The remaining genera of Onagreae (*Calylophus*, *Gaura*, *Oenothera*, *Stenosiphon*) have centers of diversity further east in North America, although *Gaura* extends into central Mexico and *Oenothera* into Central and South America. One exception to the predominantly North American nature of these tribes is *Chamerion* (the fireweeds), a genus of Epilobieae with six of its eight species and one of two sections endemic in Europe and Asia. Tribe Epilobieae definitely has a north temperate origin, with a distribution pattern that suggests a more complex history of diversification (Raven, 1976; Baum et al., 1994). All seven sections of *Epilobium* (including the former segregate genera *Boisduvalia* and *Zauschneria*) occur in or are restricted to the Madrean Region, with the large section *Epilobium* diversified on all other continents except Antarctica.

In order to seek the historical explanations that led to the high diversity and endemicity of Epilobieae, Gongylocarpeae, and Onagreae in North America, we will analyze the patterns of distribution of species of these tribes native to North America (for a list of species and references, see Table 1). A focus on patterns of distribution requires conceptual and methodological tools that allow comparisons to be made in a meaningful and informative way. Two modern approaches that allow this kind of analysis are parsimony analysis of endemicity and track compatibility analysis (panbiogeography) (Morrone & Crisci, 1990, 1995; Crisci et al., 2000, 2003).

Materials and Methods

Areas of Endemism

An area of endemism is defined as an area of nonrandom distributional congruence among different taxa. It is identified by the congruent distributional boundaries of two or more species, where congruence does not demand complete agreement on those limits at all possible scales of mapping, but relatively extensive sympatry is a prerequisite (Platnick, 1991).

Areas of endemism used in this analysis are defined primarily by Takhtajan (1986) and Thorne (1993) and validated by other biogeographical studies (i.e., Dice, 1943; Rzedowski, 1978; Brown et al., 1979, 1998; McLaughlin, 1989, 1992; Ayala et al., 1993; Escalante Pliego et al., 1993; Fa & Morales, 1993; Li & Adair, 1994; Liebherr, 1994a, b; Morrone et al., 1999; Marshall & Liebherr, 2000; Morrone, 2001). Because the focus of this study is on a major plant lineage that has diversified in arid North America, we have used small, closely defined areas within the Madrean area. Some taxa within this lineage have distributions that extend beyond the North American regions. For these we used the more broadly defined Neotropical, East Palearctic, and West Palearctic regions, since they fall outside of our area of focus in North America. Africa and Australia were not included because native North American species of these three tribes occur in these areas only as exotics. Table 2 lists the areas of endemism alphabetically, with taxa of the three target tribes endemic to each area. Full descriptions of each area of endemism, including sample plant and animal taxa endemic to each, are provided in Appendix 1. The areas are illustrated in Figure 1.

In some regions, the area delineations provided by Takhtajan (1986) and Thorne (1993) proved somewhat vague or difficult to interpret, and in those cases we used additional resources to determine the boundaries. For example, we used the geographical subdivisions found in *The Jepson Manual* (Hickman, 1993) to more precisely delineate the five regions in California (CAL, GBA, MOJ, SON, and VAN; see Table 2 for area acronyms). Similarly, we used the vegetational areas described in Correll and Johnston (1970) to establish the boundaries of the regions in Texas (APP, ATL, CHI, NAP, and TAM). Additional sources used for specific areas are referenced in the area description. In this way, distributional records could be placed more precisely in the appropriate area of endemicity.

Taxa Analyzed

The primary data for this analysis are the distributions of 173 native species of Onagraceae tribes Epilobieae, Gongylocarpeae, and Onagreae inhabiting North America (Canada, Mexico, United States; Table 1). The distributional data were taken

Table 1. List of species included in this analysis and source of distributional data (see text for details regarding unpublished data). *Gongylocarpus* is listed here in tribe Onagreae; only recently (Levin et al., 2003) it was transferred to tribe Gongylocarpeae. The number of each species corresponds with column numbers in the data matrix (Table 3). Names of taxa are those currently in use, based on recent revisions. Two of the names, *Oenothera deserticola* and *O. purpusii*, subsequently have been revised due to a nomenclatural problem (Wagner, 2004): *Oenothera purpusii* in the sense used here will become *O. deserticola*, and the current *O. deserticola* will take a new name.

Taxa	Source of information
TRIBE ONAGREAE	
Camissonia Link	Raven (1962, 1969)
1. *C. andina* (Nutt.) P. H. Raven	
2. *C. arenaria* (A. Nelson) P. H. Raven	
3. *C. boothii* (Douglas) P. H. Raven	
4. *C. breviflora* (Torr. & A. Gray) P. H. Raven	
5. *C. brevipes* (A. Gray) P. H. Raven	
6. *C. californica* (Nutt. ex Torr. & A. Gray) P. H. Raven	
7. *C. campestris* (Greene) P. H. Raven	
8. *C. cardiophylla* (Torr.) P. H. Raven	
9. *C. chamaenerioides* (A. Gray) P. H. Raven	
10. *C. cheiranthifolia* (Hornem. ex Spreng.) Raim.	
11. *C. claviformis* (Torr. & Frém.) P. H. Raven	
12. *C. confusa* P. H. Raven	
13. *C. contorta* (Douglas) Kearney	
14. *C. eastwoodiae* (Munz) P. H. Raven	
15. *C. graciliflora* (Hook. & Arn.) P. H. Raven	
16. *C. guadalupensis* (S. Watson) P. H. Raven	
17. *C. hilgardii* (Greene) P. H. Raven	
18. *C. hirtella* (Greene) P. H. Raven	
19. *C. ignota* (Jeps.) P. H. Raven	
20. *C. intermedia* P. H. Raven	
21. *C. kernensis* (Munz) P. H. Raven	
22. *C. lacustris* P. H. Raven	
23. *C. lewisii* P. H. Raven	
24. *C. minor* (A. Nelson) P. H. Raven	
25. *C. multijuga* (S. Watson) P. H. Raven	
26. *C. ovata* (Nutt. ex Torr. & A. Gray) P. H. Raven	
27. *C. pallida* (Abrams) P. H. Raven	
28. *C. palmeri* (S. Watson) P. H. Raven	
29. *C. parvula* (Nutt. ex Torr. & A. Gray) P. H. Raven	
30. *C. pterosperma* (S. Watson) P. H. Raven	
31. *C. pubens* (S. Watson) P. H. Raven	
32. *C. pusilla* P. H. Raven	
33. *C. pygmaea* (Douglas) P. H. Raven	
34. *C. refracta* (S. Watson) P. H. Raven	
35. *C. robusta* P. H. Raven	
36. *C. scapoidea* (Torr. & A. Gray) P. H. Raven	
37. *C. strigulosa* (Fisch. & C. A. Mey.) P. H. Raven	
38. *C. subacaulis* (Pursh) P. H. Raven	
39. *C. tanacetifolia* (Torr. & A. Gray) P. H. Raven	
40. *C. walkeri* (A. Nelson) P. H. Raven	
Calylophus Spach	Towner (1977)
41. *C. berlandieri* Spach	
42. *C. hartwegii* (Benth.) P. H. Raven	
43. *C. lavandulifolius* (Torr. & A. Gray) P. H. Raven	
44. *C. serrulatus* (Nutt.) P. H. Raven	
45. *C. toumeyi* (Small) Towner	
46. *C. tubicula* (A. Gray) P. H. Raven	
Clarkia Pursh	Lewis & Lewis (1955, except in *)
47. *C. amoena* (Lehm.) A. Nelson & J. F. Macbr.	

Table 1. Continued.

Taxa	Source of information
48. *C. biloba* (Durand) A. Nelson & J. F. Macbr.	
49. *C. concinna* (Fisch. & C. A. Mey.) Greene	
50. *C. cylindrica* (Jeps.) F. H. Lewis & M. R. Lewis	
51. *C. dudleyana* (Abrams) J. F. Macbr.	
52. *C. epilobioides* (Nutt. ex Torr. & A. Gray) A. Nelson & Macbr.	
53. *C. gracilis* (Piper) A. Nelson & J. F. Macbr.	
54. **C. heterandra* (Torr.) F. H. Lewis & P. H. Raven	Lewis (1993)
55. *C. lassenensis* (Eastw.) F. H. Lewis & M. R. Lewis	
56. *C. modesta* Jeps.	
57. **C. mosquini* E. Small	Lewis (1993)
58. *C. pulchella* Pursh	
59. *C. purpurea* (Curtis) A. Nelson & J. F. Macbr.	
60. *C. rhomboidea* Douglas	
61. **C. rostrata* W. S. Davis	Lewis (1993)
62. *C. speciosa* F. H. Lewis & M. R. Lewis	
63. **C. tembloriensis* Vasek	Lewis (1993)
64. *C. unguiculata* Lindl.	
65. *C. xantiana* A. Gray	
Gaura L.	Raven & Gregory (1972)
66. *G. angustifolia* Michx.	
67. *G. biennis* L.	
68. *G. boquillensis* P. H. Raven & D. P. Greg.	
69. *G. brachycarpa* Small	
70. *G. calcicola* P. H. Raven & D. P. Greg.	
71. *G. coccinea* Pursh	
72. *G. drummondii* (Spach) Torr. & A. Gray	
73. *G. filipes* Spach	
74. *G. hexandra* Ortega	
75. *G. longiflora* Spach	
76. *G. mckelveyae* (Munz) P. H. Raven & D. P. Greg.	
77. *G. mutabilis* Cav.	
78. *G. neomexicana* Wooton	
79. *G. parviflora* Douglas ex Lehm.	
80. *G. sinuata* Nutt. ex Ser.	
81. *G. suffulta* Engelm. ex A. Gray	
82. *G. villosa* Torr.	
Gayophytum A. Juss.	Lewis & Szweykowski (1964)
83. *G. decipiens* F. H. Lewis & Szweykowski	
84. *G. diffusum* Torr. & A. Gray	
85. *G. heterozygum* F. H. Lewis & Szweykowski	
86. *G. humile* A. Juss.	
87. *G. racemosum* Torr. & A. Gray	
88. *G. ramosissimum* Torr. & A. Gray	
Gongylocarpus Cham. & Schltdl. (transferred to **Gongylocarpeae**; Levin et al., 2003)	
89. *G. rubricaulis* Schltdl. & Cham.	Carlquist & Raven (1966)
Oenothera L.	
90. *O. albicaulis* Pursh	W. L. Wagner (unpublished data)
91. *O. biennis* L.	Dietrich et al. (1997)
92. *O. brachycarpa* A. Gray	W. L. Wagner (unpublished data)
93. *O. caespitosa* Nutt.	Wagner et al. (1985)
94. *O. californica* (S. Watson) S. Watson	W. L. Wagner (unpublished data)
95. *O. cavernae* Munz	Wagner et al. (1985)
96. *O. cordata* J. W. Loudon	Dietrich & Wagner (1988)
97. *O. coronopifolia* Torr. & A. Gray	W. L. Wagner (unpublished data)
98. *O. deltoides* Torr. & Frém.	W. L. Wagner (unpublished data)

Table 1. Continued.

Taxa	Source of information
99. *O. deserticola* (Loes.) Munz	Wagner (2004, unpublished data)
100. *O. dissecta* A. Gray ex S. Watson	Wagner (1984)
101. *O. drummondii* Hook.	Dietrich & Wagner (1988)
102. *O. elata* Kunth	Dietrich et al. (1997)
103. *O. epilobiifolia* Kunth	W. L. Wagner (unpublished data)
104. *O. falfurriae* W. Dietr. & W. L. Wagner	Dietrich & Wagner (1988)
105. *O. flava* (A. Nelson) Garrett	W. L. Wagner (unpublished data)
106. *O. fruticosa* L.	Straley (1977)
107. *O. grandiflora* L'Hér.	Dietrich et al. (1997)
108. *O. grandis* (Britton) Smyth	Dietrich & Wagner (1988)
109. *O. heterophylla* Spach	Dietrich & Wagner (1988)
110. *O. howardii* (A. Nelson) W. L. Wagner	W. L. Wagner (unpublished data)
111. *O. humifusa* Nutt.	Dietrich & Wagner (1988)
112. *O. jamesii* Torrey & A. Gray	Dietrich et al. (1997)
113. *O. kunthiana* (Spach) Munz	W. L. Wagner (unpublished data)
114. *O. laciniata* Hill	Dietrich & Wagner (1988)
115. *O. latifolia* (Rydb.) Munz	W. L. Wagner (unpublished data)
116. *O. linifolia* Nutt.	Straley (1977)
117. *O. longissima* Rydb.	Dietrich et al. (1997)
118. *O. macrocarpa* Nutt.	W. L. Wagner (unpublished data)
119. *O. macrosceles* A. Gray	Dietrich et al. (1985)
120. *O. mexicana* Spach	Dietrich & Wagner (1988)
121. *O. nuttallii* Sweet	W. L. Wagner (unpublished data)
122. *O. nutans* G. F. Atk. & Bartlett	Dietrich et al. (1997)
123. *O. oakesiana* (A. Gray) J. W. Robbins ex S. Watson & J. M. Coulter	Dietrich et al. (1997)
124. *O. pallida* Lindl.	W. L. Wagner (unpublished data)
125. *O. parviflora* L.	W. L. Wagner (unpublished data)
126. *O. pennellii* Munz	W. L. Wagner (unpublished data)
127. *O. perennis* L.	Straley (1977)
128. *O. pilosella* Raf.	Straley (1977)
129. *O. primiveris* A. Gray	Wagner (1986, unpublished data)
130. *O. pubescens* Willd. ex Spreng.	Dietrich & Wagner (1988)
131. *O. purpusii* Munz	Wagner (2004, unpublished data)
132. *O. rhombipetala* Nutt. ex Torr. & A. Gray	Dietrich & Wagner (1988)
133. *O. rosea* L'Hér. ex Aiton	W. L. Wagner (unpublished data)
134. *O. spachiana* Torr. & A. Gray	Straley (1977)
135. *O. speciosa* Nutt.	W. L. Wagner (unpublished data)
136. *O. tetraptera* Cav.	W. L. Wagner (unpublished data)
137. *O. triloba* Nutt.	W. L. Wagner (unpublished data)
138. *O. tubifera* Ser.	W. L. Wagner (unpublished data)
139. *O. villosa* Thunb.	W. L. Wagner (unpublished data)
Stenosiphon Spach	
140. *S. linifolius* (Nutt.) Heynh.	Great Plains Flora Assoc. (1986)
TRIBE EPILOBIEAE	
Chamerion (Raf.) Raf.	Hoch (1993)
141. *C. angustifolium* L.	Mosquin (1966)
142. *C. latifolium* L.	Small (1968)
Epilobium L.	Hoch (1986, 1993, unpublished (see text))
143. *E. anagallidifolium* Lam.	
144. *E. arcticum* Sam.	
145. *E. brachycarpum* C. Presl	
146. *E. canum* (Greene) P. H. Raven	
147. *E. ciliatum* Raf.	
148. *E. clavatum* Hausskn.	

Table 1. Continued.

Taxa	Source of information
149. *E. coloratum* Spreng.	
150. *E. davuricum* Fisch. ex Hornem.	
151. *E. densiflorum* (Lindl.) Hoch & P. H. Raven	Raven & Moore (1965)
152. *E. denticulatum* Ruiz & Pav.	
153. *E. foliosum* (Nutt. ex Torr. & A. Gray) Suksd.	
154. *E. glaberrimum* Barbey	
155. *E. halleanum* Hausskn.	
156. *E. hornemannii* Rchb.	
157. *E. lactiflorum* Hausskn.	
158. *E. leptocarpum* Hausskn.	
159. *E. leptophyllum* Raf.	
160. *E. luteum* Pursh	
161. *E. minutum* Lindl. ex Lehm.	
162. *E. mirabile* Trel.	
163. *E. nevadense* Munz	
164. *E. obcordatum* A. Gray	
165. *E. oregonense* Hausskn.	
166. *E. pallidum* (Eastw.) Hoch & P. H. Raven	Raven & Moore (1965)
167. *E. palustre* L.	
168. *E. pygmaeum* (Speg.) Hoch & P. H. Raven	Raven & Moore (1965)
169. *E. saximontanum* Hausskn.	
170. *E. smithii* H. Lév.	
171. *E. strictum* Muhl.	
172. *E. suffruticosum* Nutt.	
173. *E. torreyi* (S. Watson) Hoch & P. H. Raven	Raven & Moore (1965)

from recent or unpublished taxonomic revisions, supplemented with specimen label data from the herbaria at MO and US (Table 3). Distribution records for *Epilobium* derive from nearly 100,000 specimens from more than 100 herbaria consulted in preparation for a revision (Hoch et al., unpublished); these records served as the basis for *Epilobium* treatments in *The Jepson Manual* (Hoch, 1993), the *Flora of the Great Plains* (Hoch, 1986), and other recent floras. Records for several sections of *Oenothera* for which taxonomic revisions are not yet published (cited in Table 1 as "Wagner, unpublished data") are derived from several sources. All unpublished *Oenothera* distributions except for those of section *Anogra* are based on approximately 4500 collections from more than 100 herbaria borrowed for those revisions. For the 10 species of section *Anogra*, distributions derive from some 250 collections at US and MO, supplemented by additional collections examined for *The Jepson Manual* project (Wagner, 1993). We have excluded from our distributional analysis specimens that were cultivated and/or appear far outside the established range in human-disturbed habitats. Species that occur only in one area of endemism are not informative in a Parsimony Analysis of Endemicity (PAE) regarding area relationships and therefore are excluded from the analysis. However, they provide support for the delimitation of areas of endemism and are listed in Table 2. For example, the monotypic genus *Xylonagra* is endemic to Central Baja California and thus is used to circumscribe the Sonoran (SON) region.

Although almost all of the genera of Epilobieae, Gongylocarpeae, and Onagreae are endemic to or have had their major basal radiation in the Madrean Floristic Region of southwestern North America, many species of these tribes, especially in *Epilobium* and *Oenothera*, occur outside of North America. If native North American species also have a native distribution outside of North America, those distributions are included in the data matrix in the appropriate area (NE, WP, or EP). However, if a species occurs as a native only outside of North America, it has been excluded from this analysis. These excluded taxa include in Epilobieae 6 Eurasian species of *Chamerion* and 125 species of *Epilobium* (large groups endemic to South America, Eurasia, and Australasia), and in Onagreae, 1 species each of *Camissonia* (*C. dentata*), *Clarkia* (*C. tenella*), and *Gayophytum* (*G. micranthum*), and 39 species of *Oenothera*, virtually all endemic to South America. In *Epilobium* and *Oenothera*, we have excluded 9 species (*E. billardierianum* and *E. ko-*

Table 2. Alphabetical list of areas of endemism used in this analysis, and taxa of tribes Epilobieae, Gongylocarpeae, and Onagreae (Onagraceae) endemic to specific individual areas (see Table 1 for sources of distributional data). See Appendix 1 for full descriptions of the areas and references; numbers in parentheses refer to Appendix 1.

Acronym/Area of endemism	Endemic taxa
APP/Appalachian (3)	*Gaura demareei* P. H. Raven & D. P. Greg.; *Oenothera argillicola* Mack.
ARC/Arctic (1)	—
ATL/Atlantic and Gulf Coastal (4)	*Gaura lindheimeri* Engelm. & A. Gray; *Oenothera clelandii* W. Dietr., P. H. Raven & W. L. Wagner, *O. curtissii* Small
CAL/Californian (9)	*Camissonia benitensis* P. H. Raven, *C. bistorta* (Nutt. ex Torr. & A. Gray) P. H. Raven, *C. hardhamiae* P. H. Raven, *C. integrifolia* P. H. Raven; *C. luciae* P. H. Raven, *C. micrantha* (Hornem. ex Spreng.) P. H. Raven; *Clarkia affinis* F. H. Lewis & M. R. Lewis, *C. borealis* E. Small, *C. bottae* (Spach) F. H. Lewis & M. R. Lewis, *C. breweri* (A. Gray) Greene, *C. davyi* (Jepson) F. H. Lewis & M. R. Lewis, *C. delicata* (Abrams) A. Nelson & J. F. Macbride, *C. franciscana* F. H. Lewis & P. H. Raven, *C. imbricata* F. H. Lewis & M. R. Lewis, *C. joloensis* D. R. Parn., *C. lewisii* P. H. Raven & D. R. Parn., *C. prostrata* F. H. Lewis & M. R. Lewis, *C. rubicunda* (Lindl.) F. H. Lewis & M. R. Lewis, *C. similis* F. H. Lewis & W. R. Ernst; *Epilobium cleistogamum* (Curran) P. Hoch & P. H. Raven; *Gayophytum oligospermum* F. H. Lewis & Szweyk.
CAN/Canadian (2)	—
CHI/Chihuahuan (12)	*Gaura macrocarpa* Rothr.; *Oenothera havardii* S. Watson, *O. neomexicana* (Small) Munz, *O. organensis* Munz, *O. platanorum* P. H. Raven & D. R. Parn., *O. riskindii* W. L. Wagner, *O. texensis* P. H. Raven & D. R. Parn.
EP/East Palearctic (20)	— (some endemics, but outside of North American study group)
GBA/Great Basin (8)	*Camissonia atwoodii* Cronquist, *C. confertiflora* (P. H. Raven) P. H. Raven, *C. exilis* (P. H. Raven) P. H. Raven, *C. gouldii* P. H. Raven, *C. heterocroma* (S. Watson) P. H. Raven, *C. megalantha* (Munz) P. H. Raven, *C. nevadensis* (Kellogg) P. H. Raven, *C. parryi* (S. Watson) P. H. Raven, *C. speculicola* (P. H. Raven) P. H. Raven
MAS/Mexican Altiplano (16)	—
MOJ/Mojavean (10)	*Camissonia munzii* (P. H. Raven) P. H. Raven
NAP/North American Prairies (5)	*Gaura triangulata* Buckl.; *Oenothera canescens* Torr. & Frém., *O. coryi* W. L. Wagner, *O. engelmannii* (Small) Munz, *O. harringtonii* W. L. Wagner, Stockh. & W. M. Klein
NE/Neotropical (19)	— (some endemics, but outside of North American study group)
ROC/Rocky Mountain (7)	*Oenothera acutissima* W. L. Wagner, *O. psammophila* (A. Nelson & J. F. Macbr.) W. L. Wagner, Stockh. & W. M. Klein
SMO/Sierra Madre Occidental (14)	*Epilobium maysillesii* Munz; *Oenothera maysillesii* Munz, *O. tamrae* W. Dietr. & W. L. Wagner
SMR/Sierra Madre Oriental (17)	*Oenothera muelleri* Munz, *O. stubbei* W. Dietr., P. H. Raven & W. L. Wagner
SMS/Sierra Madre del Sur (18)	—
SON/Sonoran (11)	*Camissonia angelorum* (S. Watson) P. H. Raven, *C. crassifolia* (Greene) P. H. Raven, *C. proavita* P. H. Raven, *C. sceptrostigma* (Brandegee) P. H. Raven; *Gongylocarpus fruticulosus* (Benth.) K. Brandegee; *Oenothera arizonica* (Munz) W. L. Wagner, *O. brandegeei* (Munz) P. H. Raven, *O. breedlovei* W. Dietr. & W. L. Wagner, *O. wigginsii* W. M. Klein; *Xylonagra arborea* (Kellogg) J. D. Smith & J. N. Rose
TAM/Tamaulipan (13)	—
TMV/Trans-Mexican Volcanic Belt (15)	—
VAN/Vancouverian (6)	*Camissonia sierrae* P. H. Raven; *Clarkia arcuata* (Kellogg) A. Nelson & J. F. Macbr., *C. australis* E. Small, *C. exilis* F. H. Lewis & Vasek, *C. lingulata* F. H. Lewis & M. R. Lewis, *C. mildrediae* (Heller) F. H. Lewis & M. R. Lewis, *C. springvillensis* Vasek, *C. stellata* Mosquin, *C. virgata* Greene, *C. williamsonii* (Durand & Hilg.) F. H. Lewis & M. R. Lewis; *Epilobium howellii* P. Hoch, *E. nivium* T. S. Brandegee, *E. oreganum* Greene, *E. rigidum* Hausskn., *E. septentrionale* (D. D. Keck) Bowman & P. Hoch, *E. siskiyouense* (Munz) P. Hoch & P. H. Raven; *Gayophytum eriospermum* Coville; *Oenothera wolfii* (Munz) P. H. Raven, *O. xylocarpa* Coville
WP/West Palearctic (21)	— (some endemics, but outside of North American study group)

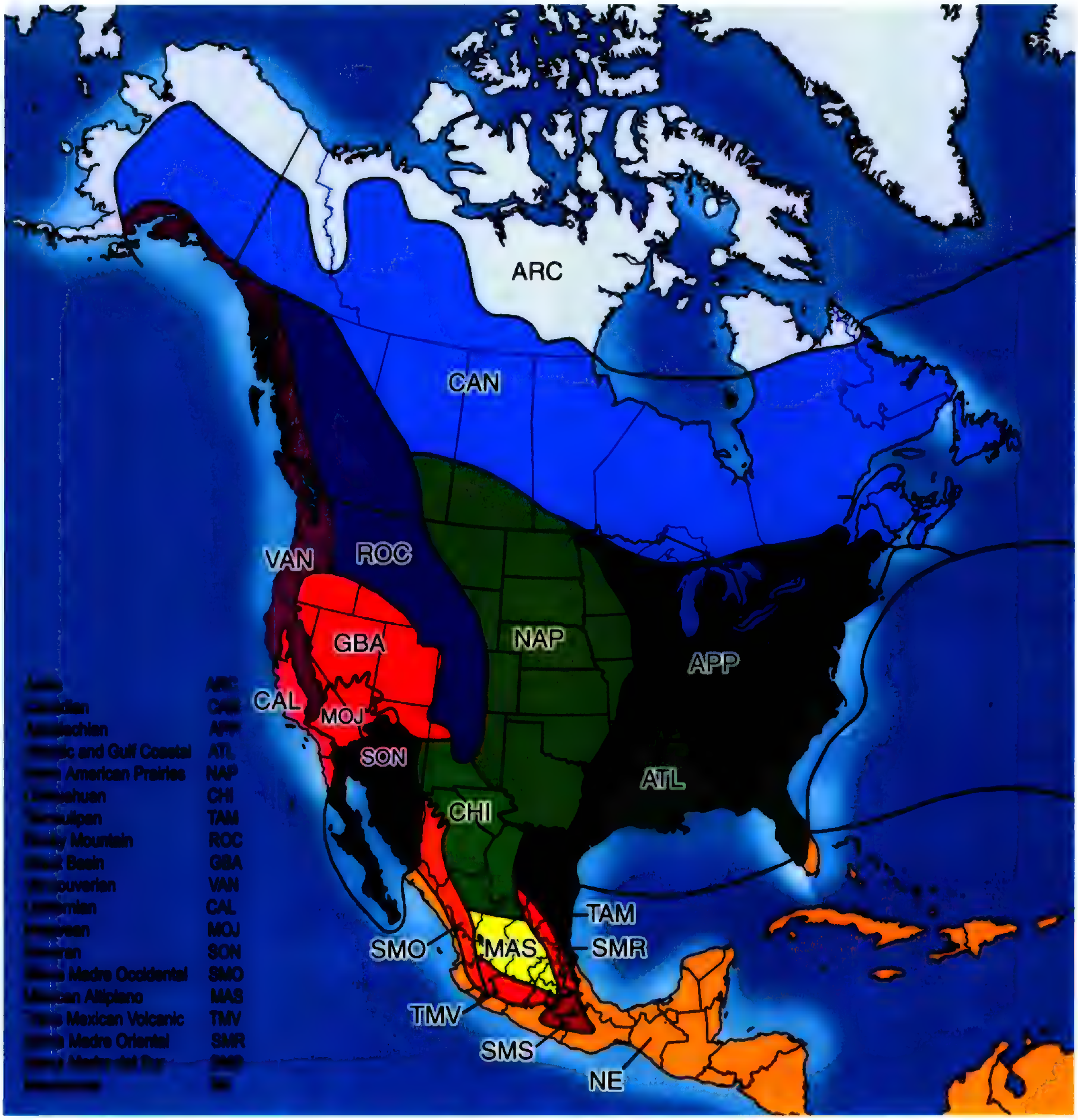

Figure 1. Areas of endemism as delimited for the historical biogeographic analysis and used to code the distributional data for each species. The areas were drawn in Photoshop 7.0 by Alice Tangerini on a base map from ArcMap 8.2 (ESRI) with a North American Lambert conformal conic projection. The floristic regions are based primarily on Takhtajan (1986) and Thorne (1993), with other modifications as described in the text.

marovianum from Australasia and *E. hirsutum*, *E. montanum*, *E. obscurum*, and *E. parviflorum* from Eurasia, *O. glazioviana*, a hybrid of recent origin in Europe, and *O. mollissima* and *O. stricta* from South America) because all of them clearly have been introduced into North America in historical time.

PARSIMONY ANALYSIS OF ENDEMICITY (PAE)

Parsimony analysis of endemicity or PAE (Rosen, 1988; Rosen & Smith, 1988) is an historical biogeographical approach that seeks to identify the distributional pattern of organisms. It classifies localities, quadrats, or areas (which are analogous to taxa) by their shared taxa (which are analogous to characters) according to the most parsimonious solution resulting in a hierarchical classification of the geographic units (Morrone & Crisci, 1995; Crisci et al., 2000, 2003). Rosen (1988) originally proposed the method using localities as study units. Craw (1988) and Cracraft (1991) presented a variation of the method using areas of endemism as study units to identify the hierarchical information contained in the geographical distribution of organ-

isms to establish area relationships. Indeed, McLaughlin (1992) suggested that areas are actually arranged in a natural hierarchy.

The variation of the methodology proposed by Craw (1988) and Cracraft (1991) using areas of endemism included taxonomic information in the matrix by adding columns for higher taxonomic categories or phylogenetic information. Thus, the resulting matrix consisted of areas × species distributions plus generic distributions. However, as Crisci et al. (2000) observed, adding phylogenetic or taxonomic information to the matrix is a misuse of Brooks parsimony analysis (Brooks et al., 2001), which is a technique that does not utilize phylogenetic data specifically. Therefore, we use areas of endemism as our units of study and species distributions as the characters of those areas, but exclude the information on supraspecific taxa.

PAE cladograms represent nested sets of areas in which terminal dichotomies represent two areas between which the most recent biotic interchange has occurred (Morrone & Crisci, 1995). Craw (1988) suggested that "character" reversions in the cladogram could be interpreted biogeographically as extinctions, and parallelisms as dispersions. This analysis was carried out using PAUP*, vers. 4.0b10 (Swofford, 2001), applying the branch-and-bound and deltran options. If more than one tree results from the analysis, a strict consensus tree is constructed. As proposed by Rosen (1988), the cladogram was rooted with a hypothetical area coded with all zeros. The bootstrap method (Felsenstein, 1985) was employed to evaluate the reliability of the estimates; 100 replicates were performed. We used the software MacClade 4.0 (Maddison & Maddison, 2000) to generate the data matrix and as a tool to analyze the taxa distribution on the tree(s).

PANBIOGEOGRAPHY (COMPATIBILITY TRACK METHOD)

Croizat (1958) postulated that geographic barriers evolve together with biotas. The panbiogeographic approach (Croizat, 1958, 1981) consists of plotting distributions of taxa on maps and connecting their separate distributional areas together with lines called individual tracks. When individual tracks coincide, the resulting summary lines are considered generalized tracks, which indicate the pre-existence of ancestral biotas that became fragmented by tectonic and/or climatic changes. At the same time, generalized tracks provide spatial criteria for biogeographic homology (Grehan, 1988a, b; Morrone & Crisci, 1995). When two or more generalized tracks intersect, that area is called a node. Nodes are dynamic biogeographic boundaries where remnant fragments of different ancestral biotas come into contact. Nodes are biogeographically interesting because they are composite regions that represent an intersection of different biogeographical and ecological histories.

Analytical developments by McAllister et al. (1986), Page (1987), Connor (1988), Craw (1989), and Henderson (1990, 1991) used graph theory to provide objective and quantitative methods for drawing and comparing tracks, including the compatibility track method applied here. This method was developed by Craw (1988, 1989), based on the concept of distributional compatibility (Connor, 1988; Craw, 1989). Individual tracks are treated as biogeographic hypotheses of relationship among localities or distribution areas. Two or more individual tracks are regarded as being compatible only if they result in the same pairwise comparison or if one track is a subset of the other. This method is analogous to character compatibility (Meacham, 1984). However, in the track compatibility method, nonoverlapping tracks are incompatible, whereas they would be compatible under the original taxonomic concept. The compatibility track method basically consists of constructing a matrix (areas vs. taxa), where each taxon is scored as present (1) or absent (0) in each area, and applying compatibility analysis software to find the largest clique(s) of compatible tracks. The method involves finding a simple form of spanning tree linking localities or distribution areas. The tree is constructed from the largest clique of compatible distributions in a distributional compatibility matrix and is based on the original concept of compatibility (nonoverlapping tracks are also considered compatible). Therefore, using a restricted concept of compatibility (only individual tracks that are either included within or replicated by one another are compatible) the tree (= clique) could contain more than one generalized track. In this case, multiple generalized tracks (groups) found in one clique will be formed only by areas that are exclusive of each generalized track. If more than one largest clique or several cliques of considerable size are found, then a hypothesis of existence of several generalized tracks linking the localities or distribution areas in more than one way can be considered (areas can be members of more than one generalized track at the same time). Alternatively, the intersection (i.e., those individual tracks common to all the largest cliques) can also be identified as a generalized track (Craw, 1990). For more details and other applications of this method see Craw (1988, 1989), Morrone and Crisci

Table 3. Data matrix (geographical areas vs. individual taxa of Onagraceae) for the compatibility track analysis and parsimony analysis of endemicity. OUT = Outgroup; other area acronyms are as listed in Table 2 and Appendix 1. Taxon number corresponds to those found in Table 1. Absence = 0; presence = 1.

	10	20	30	40	50	60	70	80	90
OUT	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
ARC	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
CAN	0001000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	1000000000	0000000000
APP	0000000000	0000000000	0000000000	0000000000	1101000000	0000000000	0000001010	0110110011	1000000000
ATL	0000000000	0000000000	0000000000	0000000000	1101000000	0000000000	0000011010	0110110011	1000000000
NAP	1001000000	0000000000	0000000000	0000010100	1111010000	0000000100	0000001011	1100100111	1101001101
VAN	1010001001	1010101110	1101010101	1111000110	0000001111	1011111111	1111100000	0000000000	0011111100
ROC	1011000000	0011001000	0001000010	0110010111	0111000000	0010000101	0000000000	1000000110	0011011101
GBA	1011100010	1001000000	0001101111	1111010111	0110000000	0010100101	0000000000	1001000010	0011111101
CAL	0110111001	1110110111	1110011100	1001101000	0000001111	1111111011	1111100000	0000000000	0011111000
MOJ	0010110110	1000000000	1000101101	0101000001	0010000000	0000000000	0000000000	1000000010	0000000001
SON	0110110111	1100010111	0010001000	0001101000	0011100000	0100000011	0000000000	1001001010	0010000101
CHI	0000000010	0000000000	0000000000	0000000000	1111110000	0000000000	0000000101	1101001111	1100000001
TAM	0000000000	0000000000	0000000000	0000000000	1111010000	0000000000	0000000111	1100110011	1100000010
SMO	0000000000	0000000000	0000000000	0000000000	0000100000	0000000000	0000000000	1001001010	0000000010
TMV	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	1101001010	0000000010
MAS	0000000000	0000000000	0000000000	0000000000	0100000000	0000000000	0000000000	1101001000	0000000010
SMR	0000000000	0000000000	0000000000	0000000000	0100010000	0000000000	0000000000	1001001000	0000000000
SMS	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	1100001000	0000000000
NE	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000010000	0001000000	0000010010
WP	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
EP	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000

Table 3. Continued.

	100	110	120	130	140	150	160	170	173
OUT	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	000
ARC	0000000000	0000000000	0000000000	0000000000	0000000000	1111001001	0000011111	0000001010	000
CAN	1000000000	0000010000	0000000000	0010101100	0000000010	1111101011	0000011010	0000001010	100
APP	1000010000	0101011110	0101010101	1110101100	0101111011	1000101010	0000000010	0000001000	100
ATL	1000010000	1001011110	1101010101	0110101100	0011110010	1000001010	0000000010	0000001000	100
NAP	1010001000	0101110111	0111110100	1001100000	0101101011	1000101010	0000111010	0000001110	000
VAN	0000000100	0100100000	0000000000	0001000000	0000000010	1110111100	1011111111	1101111111	001
ROC	0010001000	0100100000	0000101000	1001000001	0000000010	1110111101	1011111111	1101101111	011
GBA	0011101100	0100100001	0000101000	0001000011	0000000010	1110111100	1001111010	1011111110	011
CAL	0001000100	0100100000	0000000000	0000000000	0000000000	1110111100	1011111010	1000111100	001
MOJ	0011101100	0000100001	0000001000	0000000011	0000000000	1000111000	0000000000	0010000000	000
SON	0111000100	1100100000	0010000000	0001000011	0010001000	0000111000	1011000000	0000000000	000
CHI	0110001001	0100100000	0111000110	0001010011	0110101011	1000111000	0000000000	0000000010	000
TAM	0100000000	1001000100	0111000010	0000010001	0010111000	0000000000	0000000000	0000000000	000
SMO	0000000000	0100100000	0010000000	0000000001	0010010100	0000001000	0000000000	0000000000	000
TMV	0000000000	0000000000	0010000000	0000000001	1010010100	0000001000	0100000000	0000000000	000
MAS	0000000011	0110100000	0110000000	0000000001	1010010100	0000001000	0100000000	0000000000	000
SMR	0000000010	0110000000	0010000000	0000000001	1010010100	0000001000	0000000000	0000000000	000
SMS	0000000000	0110000000	0010000000	0000000001	1010010000	0000001000	0100000000	0000000000	000
NE	0000000010	0110000000	1011000000	0000000001	0010000000	0000001010	0100000000	0000000000	000
WP	0000000000	0000000000	0000000000	0000000000	0000000000	1111000001	0000011000	0000001000	000
EP	0000000000	0000000000	0000000000	0000000000	0000000000	1111001001	0000011000	0000001000	000

(1990, 1995), Craw et al. (1999), and Crisci et al. (2000, 2003).

In this analysis we use the same areas of endemism and the same data matrix (Table 3) that we used in the PAE analysis. The analysis of the data matrix of 21 areas of endemism versus individual tracks of 173 taxa (Table 3) was carried out with SECANT 2.2 (Salisbury, 1999). SECANT identifies all groups of cladistically compatible characters. Individual tracks were treated here as binary characters ordered with absence as the "ancestral" state for each (= outgroup with all zeros), and presence as state 1.

Results

PARSIMONY ANALYSIS OF ENDEMICITY

The analysis of the data matrix (Table 3) with PAUP*4.0b10 generated four area cladograms (Fig. 2) with 377 steps, consistency index (CI) = 0.459, and retention index (RI) = 0.619, which differed in the relationships among most Mexican areas SMO, TMV, MAS, SMR, SMS; in the relationship of the Neotropical area (NE) either with the Mexican areas (Fig. 2B–D) or with the eastern North American areas APP, ATL, NAP, CHI, and TAM (Fig. 2A); in the relationship of APP, ATL, NAP, CHI, and TAM either with the Mexican areas (Fig. 2A–B) or with the western areas VAN, CAL, ROC, GBA, SON, and MOJ (Fig. 2C–D); and in the relationship of Tamaulipas (TAM) either with Chihuahua (CHI) (Fig. 2C–D), or with APP, ATL, NAP, and CHI (Fig. 2A–B).

The strict consensus of the four trees (Fig. 3) shows the following area relationships: (1) ((Arctic, Canadian) West Palearctic, East Palearctic) forms the basalmost lineage, sister to the remaining areas; (2) (((Appalachian, Atlantic) North American Prairies) Chihuahuan, Tamaulipas); (3) ((((Vancouverian, Californian) (Rocky Mountains, Great Basin)) Sonoran) Mojavean); (4) ((Mexican Altiplano, Sierra Madre Oriental) Sierra Madre Occidental, Trans-Mexican Volcanic Belt, Sierra Madre del Sur); and (5) the Neotropical as one single branch. The last four branches (2–5) constitute a polytomy. Thus, the strict consensus cladogram generated by PAUP*4.0b10 shows four main groups (Fig. 4): northern North America, eastern North America, western North America, and the central Mexican areas.

The percentage of 100 bootstrap replicates demonstrates that strength of support for nodes varies considerably. Many branches have less than 50% support, but others, particularly in eastern and western North America, have stronger support. The most strongly supported branches in order are: 99% (APP—ATL), 98% (VAN—CAL), 96% (VAN, CAL, ROC, GBA), 79% (ROC—GBA), 78% (APP, ATL, NAP, CHI, TAM), 62% (VAN, CAL, ROC, GBA, SON, MOJ), 61% (APP, ATL, NAP), and 60% (ARC, CAN, WP, EP). The weakness and strength of bootstrap values may reflect the strong concentration of taxa in northern Mexico and southwestern United States, and lower concentration in areas more distant from that area.

PANBIOGEOGRAPHY (COMPATIBILITY TRACK METHOD)

Applying the SECANT 2.2 program to the data matrix (Table 3) resulted in 4 largest cliques, each with 51 individual tracks. The intersection (those 49 individual tracks common to the 4 largest cliques) is considered as the fifth large clique. These 5 cliques contain a total of 11 generalized tracks. The first clique contains 2 generalized tracks, the second clique contains 2, the third clique contains 3, the fourth clique contains 2, and the intersection contains 2 generalized tracks. Since many of these tracks in different cliques are the same, the 11 generalized tracks can be reduced to 3 generalized tracks: 2 strongly supported ("East"/green and "West"/purple in Fig. 5), and 1 weakly supported ("South"/orange in Fig. 5). The northern regions (ARC, CAN, EP, and WP) and two areas in Mexico (SMO and TMV) are not part of these supported generalized tracks, and are shown as white in Figure 5.

The first ("East") strong generalized track includes eastern North American areas (ATL, APP, CHI, NAP, TAM), and is strongly supported by 17 individual tracks from taxa in 3 genera, namely, *Calylophus berlandieri* (taxon 41); *Gaura biennis* (67), *G. brachycarpa* (69), *G. filipes* (73), *G. longiflora* (75), *G. sinuata* (80), and *G. suffulta* (81); and *Oenothera cordata* (96), *O. falfurriae* (104), *O. grandiflora* (107), *O. grandis* (108), *O. heterophylla* (109), *O. linifolia* (116), *O. mexicana* (120), *O. nutans* (122), *O. spachiana* (134), and *O. speciosa* (135).

The second ("West") strong generalized track includes the western North American areas (CAL, GBA, MOJ, ROC, SON, VAN), and is supported by 31 individual tracks from taxa in 4 genera, namely, *Camissonia boothii* (taxon 3), *C. campestris* (7), *C. graciliflora* (15), *C. lacustris* (22), *C. ovata* (26), and *C. pubens* (26); all species of *Clarkia* (47–65) except for *C. epilobioides* (52), *C. pulchella* (58), and *C. purpurea* (59); *Gayophytum decipiens* (83) and *G. heterozygum* (85); and *Epilobium clavatum* (148), *E.*

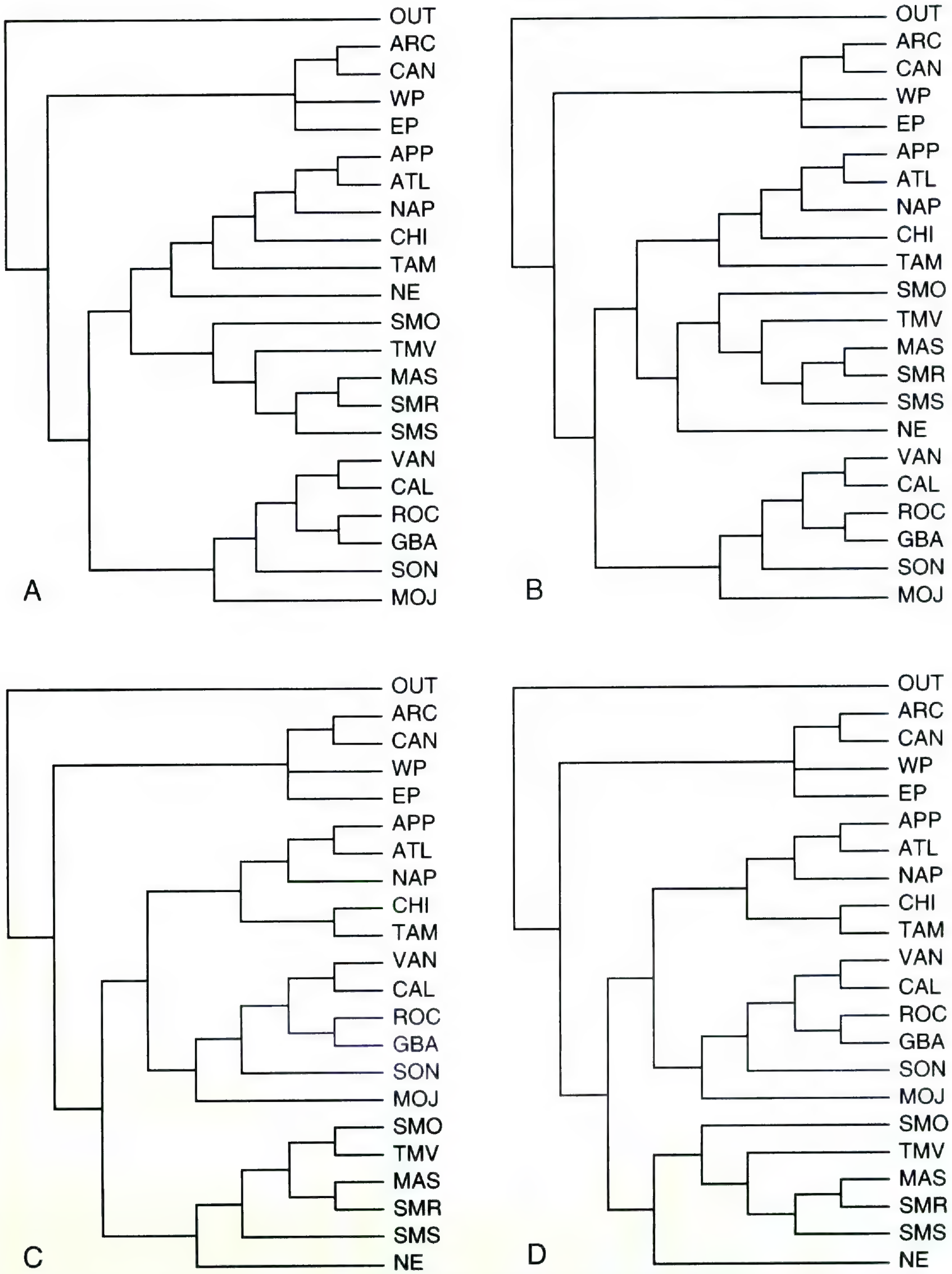

Figure 2. Four most parsimonious cladograms (A–D) resulting from the parsimony analysis of endemicity (PAE) analysis after applying PAUP* vers. 4.0b10. Trees are 377 steps, CI = 0.459, and RI = 0.619. Area acronyms correspond to those in Figure 1 and Table 2.

Strict

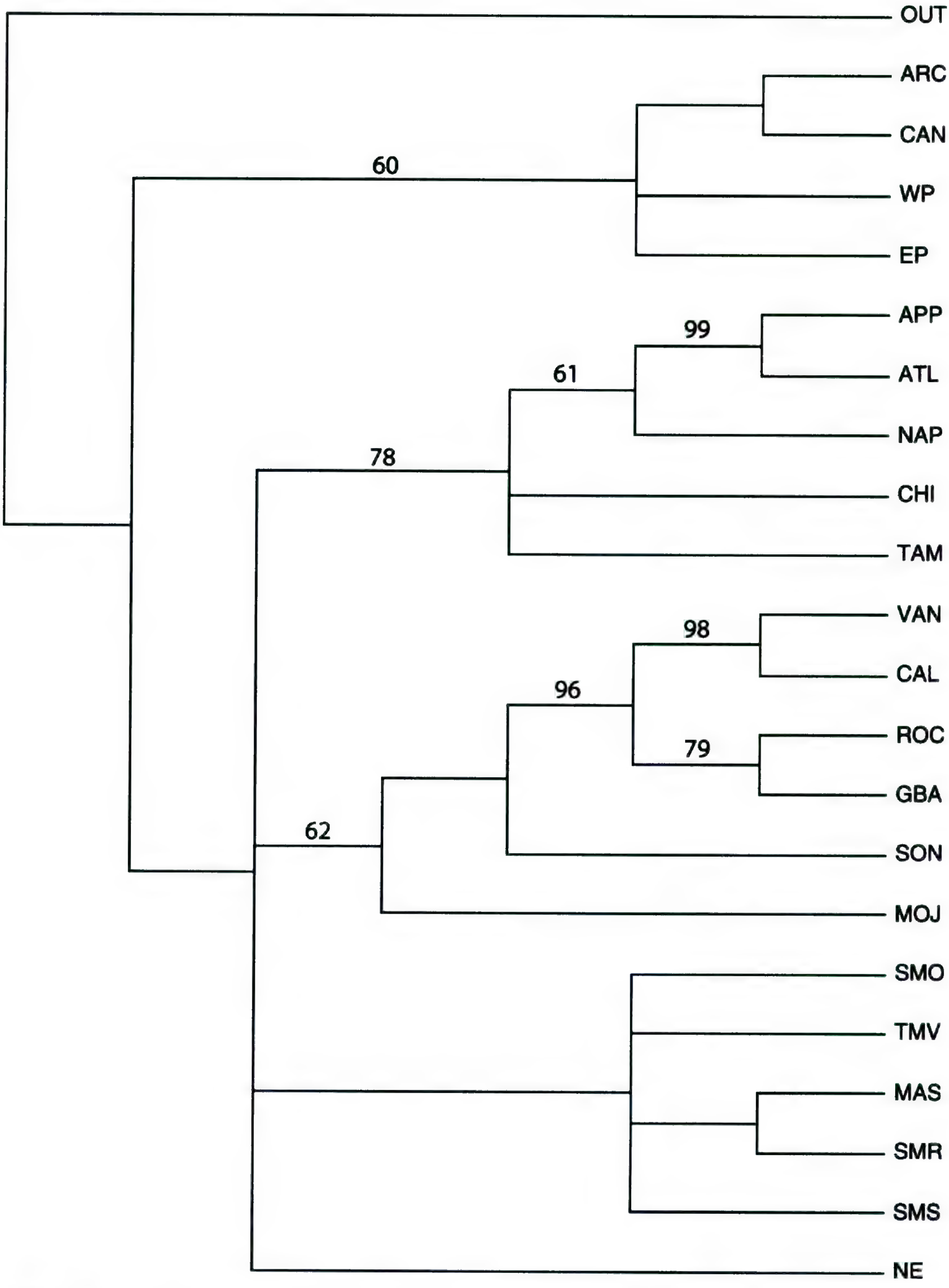

Figure 3. Strict consensus cladogram of the four cladograms obtained in the parsimony analysis of endemicity (PAE). Bootstrap support values are shown above the branches. Area acronyms correspond to those in Figure 1 and Table 2.

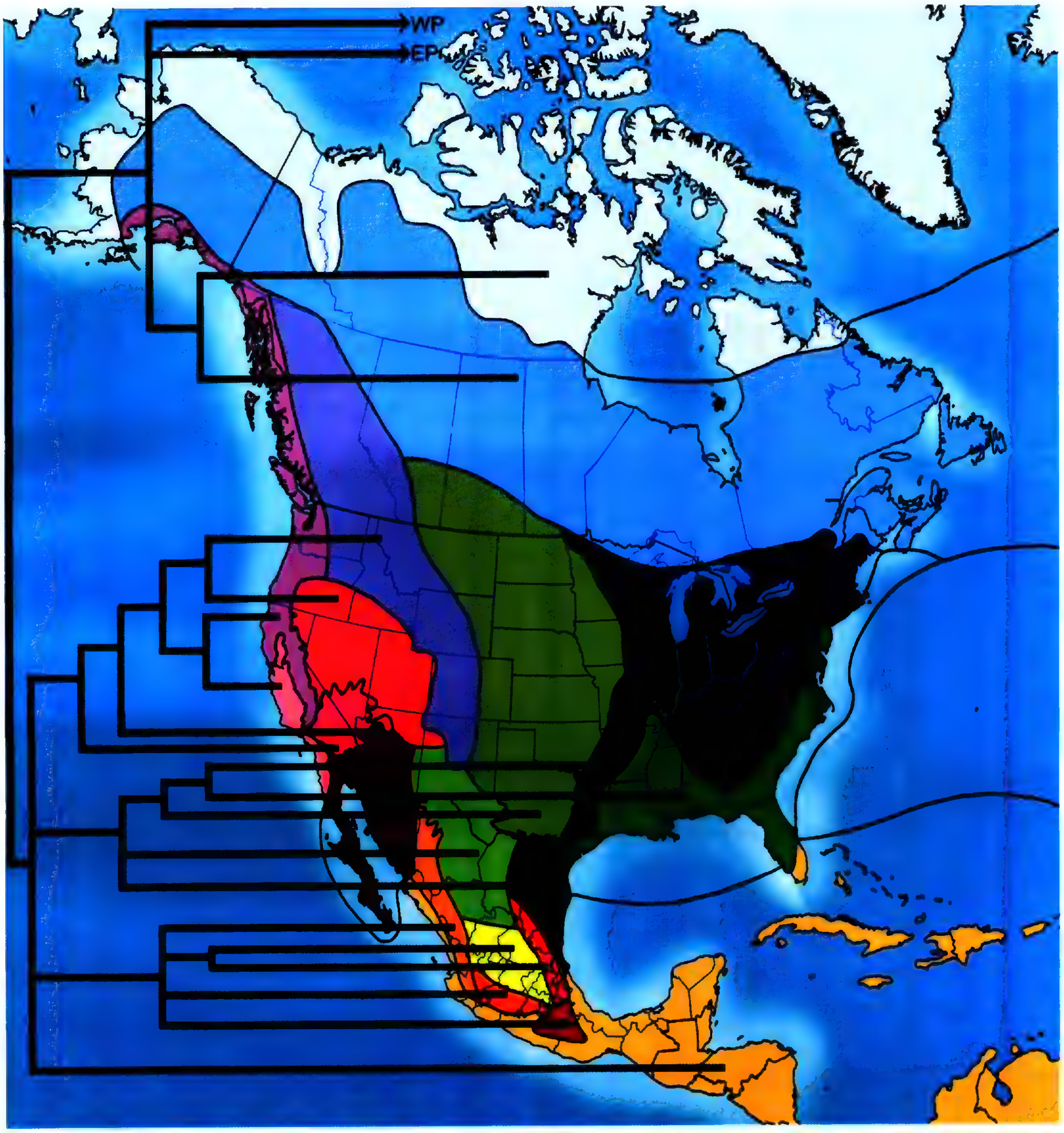

Figure 4. Strict consensus cladogram of the four cladograms obtained in the parsimony analysis of endemicity superimposed onto the map with the areas of endemism. The tree branches delineate four main groups of areas: northern (ARC, CAN, EP, WP), eastern North America (APP, ATL, NAP, CHI, TAM), western North America (VAN, CAL, ROC, GBA, SON, MOJ), and southern North America (SMO, TMV, MAS, SMR, SMS). Areas correspond to those in Figure 1 and Table 2.

densiflorum (151), *E. glaberrimum* (154), *E. minutum* (161), *E. oregonense* (165), *E. pallidum* (166), and *E. torreyi* (173).

The third ("South") generalized track includes some of the Mexican areas (MAS, SMR, SMS) and the Neotropical area (NE), with support from only 2 individual tracks, of *Oenothera deserticola* (taxon 99) and *O. epilobiifolia* (103). The South generalized track is considerably weaker than the previous two, since it is supported by many fewer individual tracks. The Neotropical area is supported as part of the East generalized track by *Oenothera laciniata* (taxon 114). The Trans-Mexican Volcanic Belt (TMV) is supported as part of the South generalized track by *Oenothera kunthiana* (taxon 113). Several Mexican areas (SMS, TMV, MAS) are supported as part of the East generalized track by *Gaura drummondii* (taxon 72) and *Oenothera jamesii* (112). As noted above, the Sierra Madre Occidental (SMO) does not form part of any generalized track.

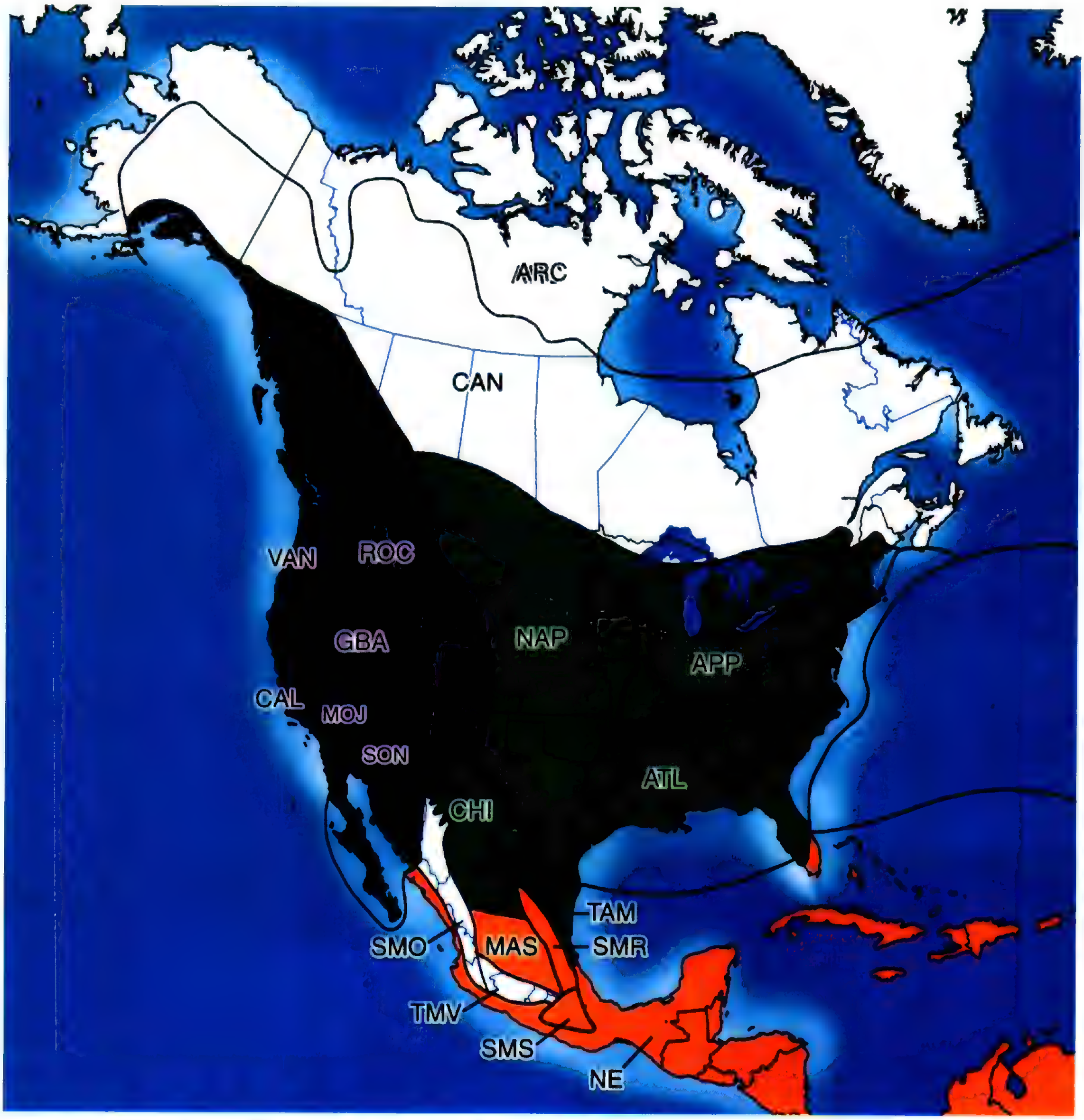

Figure 5. Distributional patterns after applying track compatibility analysis: a strongly supported Eastern generalized track including APP, ATL, CHI, NAP, and TAM, shown in green; a strongly supported Western generalized track, including CAL, GBA, MOJ, ROC, SON, and VAN, shown in purple; and a weakly supported Mexican and Neotropic generalized track including MAS, NE, SMR, and SMS, shown in orange. The areas ARC, CAN, SMO, and TMV, shown in white, and the two non-North American areas EP and WP, do not form part of any generalized track. Area acronyms correspond to those in Figure 1 and Table 2.

These data weakly support the Neotropical area (NE) as a panbiogeographic node in the distributional history of Onagreae, Gongylocarpeae, and Epilobieae, since there is some support for its inclusion in both the East and South generalized tracks.

The program SECANT 2.2 also found 9 cliques each with 50 individual tracks. The analysis of these 9 cliques resulted in the same generalized tracks that we found among the five largest cliques, with the exception of one generalized track found in only one of the 9 cliques. This additional track includes the areas CHI and TAM, supported by *Gaura boquillensis* (taxon 68), *Oenothera macrosceles* (119), and *O. pennellii* (126).

Most of the genera of Epilobieae and Onagreae support at least one of the generalized tracks found in this analysis, i.e., *Calylophus*, *Gaura*, and *Oenothera* belong to the East track, and *Camissonia*, *Clarkia*, *Gayophytum*, and *Epilobium* to the West track. Several other genera, including *Chamerion* (Epilobieae; two species), *Gongylocarpus* (Gongy-

locarpeae; two species), and *Stenosiphon* (Onagreae; one species) do not form part of any generalized track.

Discussion

The historical biogeography of North America has long been a focus of botanists attempting to find general patterns of relationships within North America and between North America and other continents. The present-day geographical distribution of Epilobieae, Gongylocarpeae, and Onagreae and the biogeographic patterns generated by those distributions may provide clues to understanding the high diversity and endemicity of these three tribes in North America, as well as the history of the areas involved.

DISTRIBUTIONAL PATTERNS

The application of Parsimony Analysis of Endemicity (PAE) to the species distribution of Epilobieae, Gongylocarpeae, and Onagreae delimits four major regions: northern North America; eastern North America; western North America; and central Mexico (Fig. 4). Three of them (eastern North America, western North America, and central Mexico) are also found in the compatibility track analysis. Comparison of these with the higher regional floristic categories in the schemes of Takhtajan (1986) and Thorne (1993) suggests the following differences and similarities. (1) Our northern North American region coincides with the Circumboreal region of Takhtajan and Thorne. (2) Our eastern North American region corresponds to the North American Atlantic region of Takhtajan and Thorne, with the addition of the Tamaulipas (TAM) and Chihuahua (CHI) areas. Miranda and Sharp (1950) proposed such an affinity from distributions of many plant species, and they and Berry (1930) suggested that this shared flora was derived from the Eocene Wilcox flora of the Mississippi Embayment. (3) The Rocky Mountain and Madrean regions of Takhtajan and Thorne show different affinities in our analysis. Their regions proposed close affinities between ROC and VAN, and among CAL, GBA, and the Sonoran Province, whereas our results link VAN with CAL and ROC with GBA. Raven and Axelrod (1978) considered the Vancouverian (VAN) and Californian (CAL) areas to be closely related since they share a flora comprising a mixture of northern temperate elements and xeric, southern elements, with a very high degree of endemism. Furthermore, Axelrod and Raven (1985) also considered the Rocky Mountains (ROC) and Great Basin (GBA) areas to be close because Cordilleran taxa spread into the western Great Basin largely after 14 m.y. ago as the climate became drier, summer rains decreased, and eastern exotic taxa were eliminated. (4) Our central Mexican areas coincide with the Mexican Highlands Province of Takhtajan and Thorne. The lower level of resolution among the central Mexican areas observed in the consensus PAE cladogram is most likely due to the relatively few species of Epilobieae, Gongylocarpeae, and Onagreae distributed there.

The relationships of the Madrean and other North American regions to the Neotropical (NE) are particularly complex, which is reflected in the ambiguous position of NE in the four shortest trees (Fig. 2). Indeed, NE could be considered a panbiogeographic node in our study. Three species (*Gaura angustifolia* [taxon 66], *Oenothera humifusa* [111], and *O. laciniata* [114]) otherwise restricted to the East region reach NE only at the southern tip of Florida, and another eastern species, *Epilobium coloratum* (149), occurs on Hispaniola (in NE), apparently by long-distance dispersal. These taxa provide support for NE as sister to the East region (Fig. 2A). A single species, *Gayophytum humile* (86), found primarily in the western region (VAN-CAL-ROC-GBA), also occurs in NE, apparently as a result of long-distance dispersal to central Chile and Argentina (Lewis & Szweykowski, 1964). Most of the connections of North American regions with NE, however, are through the Mexican region (Fig. 2B–D), almost always by close adjacent dispersal in western and southern Mexico, extending south to Central and sometimes South America. Recent phylogenetic analysis of Onagraceae (Levin et al., 2003, 2004) suggests the following: (1) the immediate sister clade to the Gongylocarpeae + Epilobieae + Onagreae is a branch with *Lopezia* (Lopezieae) and *Megacorax* (unplaced), both found primarily or exclusively in the central Mexican region, with some *Lopezia* species extending to NE; and (2) each of the three successive basal clades of the family, namely *Fuchsia* + *Circaea*, *Hauya*, and *Ludwigia*, have primary or exclusive distributions in NE. *Circaea*, with its circumboreal distribution and absence from NE, is a notable exception; however, it forms a strongly supported clade with *Fuchsia*. A detailed analysis of biogeographical patterns in Onagraceae using phylogenetic information is now in progress.

The distributions of numerous species do not coincide with the major patterns found in the PAE and track compatibility analysis. In general, these inconsistencies can result from one of three types of processes, namely, dispersal, vicariance, or extinction affecting one or few species. The predom-

inant process in our study appears to be short-distance dispersal into geographically contiguous but unrelated areas. This may involve large-scale dispersal, but more often involves only a few or even one population(s) in the adjacent area. For example, many species with distributions in the East North American region often extend into the CAN area [North region; e.g., *Oenothera biennis* (91), *O. fruticosa* (106), *O. parviflora* (125)], or into ROC [West region; e.g., *Calylophus serrulatus* (44), *Oenothera nuttallii* (121)], or to the south into the Mexican region [e.g., *Gaura drummondii* (72), *Oenothera jamesii* (112)]. Similarly, some western species reach CAN [*Camissonia breviflora* (4)] or even ARC [along the southwest coast of Alaska; *Epilobium leptocarpum* (158), *E. luteum* (160)] in the northern region, or CHI [*Camissonia chamaenerioides* (9), *Epilobium canum* (146)] or NAP [*Camissonia andina* (1), *C. subacaulis* (38), *Gayophytum ramosissimum* (88)] in the East region. One particularly clear example of adjacent dispersal concerns *Oenothera primiveris* (129); in the West region of primary distribution (GBA, SON, MOJ), most populations are large-flowered and outcrossing (including some that are self-incompatible), whereas the populations in CHI (East region) are small-flowered and autogamous (Wagner, unpublished data).

Some distributions that seem to represent adjacent dispersal may in fact have another explanation. For example, *Oenothera villosa* (taxon 139) occurs widely in both the western and eastern regions, suggesting adjacent dispersal. However, genome and cytological analysis (Dietrich et al., 1997) of this permanent translocation heterozygote species shows that populations in the western and eastern regions, which currently are treated as subspecies, derived independently from different populations of *Oenothera elata* (102). Nevertheless, they intergrade so extensively in the transition area between ROC and NAP that they are best treated as subspecies of a single species.

Several taxa may represent examples of long-distance dispersal. For example, *Epilobium saximontanum* (169), found primarily in the western region (ROC, GBA, VAN) with near outliers in the eastern region (NAP, CHI), also occurs in eastern CAN (Newfoundland) and ARC (Ungava Bay, Quebec) in the northern region. This highly disjunct pattern is not found in other species and seems best explained as a case of long-distance dispersal. The distribution of *Calylophus lavandulifolius* (43) is unusual in several ways: it appears "bimodal," with concentrations of populations in NAP (eastern) and GBA (western) and relatively few populations in intervening areas. In addition, the apparently normal distribution in NAP + CHI + TAM in the eastern region masks a long-distance disjunction between populations in northern CHI and southern TAM.

Certain recurring inconsistent distribution patterns may represent vicariance events. One pattern [found in *Clarkia pulchella* (58) and three *Epilobium*—*E. hornemannii* (156), *E. lactiflorum* (157), and *E. saximontanum* (169)] concerns the occurrence of outlier populations of western taxa (in ROC and VAN) in the Black Hills of South Dakota in NAP (East region). The Black Hills, home to numerous disjunct montane and northern taxa (e.g., Asteraceae: *Balsamorhiza sagittata*; Pinaceae: *Pinus contorta, P. flexilis*; Ranunculaceae: *Aconitum columbianum*; Van Bruggen, 1976; Great Plains Flora Association, 1986), have become isolated as the climate warmed in postglacial times; the pattern seems best explained as an example of vicariance. Similarly, at least six taxa (*Camissonia confusa* [12], three *Clarkia*—*C. epilobioides* [52], *C. purpurea* [59], and *C. rhomboidea* [60], and two *Epilobium*—*E. foliosum* [153] and *E. glaberrimum* [154]) show strongly disjunct distributions from southern California (CAL and/or VAN) to south-central Arizona (SON), mirroring a "trans-Sonoran Desert" vicariance event described by Axelrod (1979).

Finally, the absence of taxa from certain areas in which they may otherwise be anticipated may represent cases of local extinction. These are, however, difficult to prove, and in some cases clearly do not represent extinctions. For example, some species [4 of *Camissonia*—*C. brevipes* (5), *C. claviformis* (11), *C. pallida* (27), and *C. refracta* (34) and 2 of *Oenothera*—*O. californica* (94) and *O. deltoides* (98)] otherwise widespread in the western region are missing in ROC. Yet their absence in ROC cannot be considered extinctions, since all of these are desert taxa with southwestern distributions quite distant from the ROC boundaries. On the other hand, many taxa with the CAL + VAN (17 taxa) or CAL + VAN + SON (3 taxa) distribution patterns may have become extinct in the adjacent MOJ area, which has become progressively more extreme in Holocene time, and progressively inhospitable to many species (Axelrod, 1979). The absence of many taxa in the MOJ region may have forced MOJ into the position as the sister group to the rest of the western region, when it may in fact be a more recently derived area (Van Devender & Spaulding, 1979).

The establishment of western and eastern North American major regions found by PAE and track compatibility analysis agrees with many previous analyses (e.g., Li, 1952; Croizat, 1965; Graham, 1972; Iltis, 1983; Xiang et al., 1998, 2000; Wen,

1999; Guo & Ricklefs, 2000; Donoghue et al., 2001; Sanmartín et al., 2001). These analyses have defined the two broad biogeographic units based on the distributions of many taxa, some of which were evaluated in a phylogenetic context. In many of those analyses, however, there exists a relationship of these areas with East Asia. Disjunct North American–Asian taxa have been considered as Tertiary relics with former widespread distributions during the Paleogene. This "Arcto-Tertiary geoflora" (Wolfe, 1978; Larsen, 1980) resulted from migrations between eastern Asia and North America through Beringia or across the north Atlantic. The distributional patterns of Epilobieae, Gongylocarpeae, and Onagreae show a close relationship between eastern and western North America, with both areas more related to the Neotropics than to the Palearctic, and a weak association between northern North America and Asia. Our results do not reject other hypotheses of such continental connections. The taxa of Onagraceae chosen for our analysis—the tribes Epilobieae, Gongylocarpeae, and Onagreae—display a biogeographical history that may differ from those of other taxa, but that can coexist at the same time. Our analysis does not disprove the migration of taxa (including Epilobieae, Gongylocarpeae, and Onagreae) through the Bering and Atlantic northern land bridges, or through the Panama isthmus. The East and West tracks show that two ancestral biotas existed on both sides of North America, with the species of each track sharing a common distributional history.

CORRELATION OF BIOGEOGRAPHIC PATTERN WITH GEOLOGIC AND PALEOCLIMATIC EVIDENCE

The geological and climatic processes in the past provide at least partial explanations for the current biogeographical patterns in North America of Epilobieae, Gongylocarpeae, and Onagreae. Major historical events in this area include orogenic processes such as the uplifting of the Rocky Mountains, the Sierra Madre, and western Cordillera, and the most recent glaciations (summary in Graham, 1999).

The uplifting of the Rocky Mountains together with the uplifting of the Sierra Madre Occidental in the early Tertiary remarkably changed the biota of western North America, creating a barrier for floristic exchanges between eastern and western North America. This had two main effects on the flora of western North America: significant extinction of taxa because of the increasingly dry climate, and accelerated speciation and diversification of new taxa (Qian, 2001). Indeed, the area of the southern Rocky Mountains and the Sierra Madre Occidental was an important center for the evolution of the Madro-Tertiary geoflora (Axelrod, 1958). The early diversification of Onagraceae tribe Onagreae was postulated to have taken place in the Madrean vegetation of western North America (Raven & Axelrod, 1978). Until recently, tribe Gongylocarpeae, also endemic to the Madrean region, was considered to be the basal branch of Onagreae (Carlquist & Raven, 1966). Tribe Epilobieae also may have originated in western North America as part of the Madro-Tertiary geoflora (Raven, 1976; Baum et al., 1994), but evidence from fossil pollen is equivocal, and the distribution of *Chamerion* and its position as sister to *Epilobium* (Baum et al., 1994) suggest a possible origin in western Eurasia (Raven & Raven, 1976). The strong association of *Epilobium* to the western track, and the endemism of the near-basal species *E. rigidum* (Baum et al., 1994; Levin et al., 2004) in the VAN region, support an origin of the genus in western North America. The Madro-Tertiary geoflora had already appeared on the drier borders of the North American tropics by the Middle Eocene, and probably occupied much of the southwestern United States and adjacent Mexico by the close of the Oligocene. It extended its range in all directions in response to the expanding aridity in the succeeding Miocene epoch (Axelrod, 1958; Valliente-Banuet et al., 1998). Major expansion of Onagraceae tribes Onagreae, Gongylocarpeae, and Epilobieae may have occurred during the Miocene and Pliocene (Raven & Axelrod, 1974; Raven & Raven, 1976; Raven, 1979).

From the late Oligocene (25 mya) through the Pliocene, new orogeny gave rise to the present western Cordilleran System, including major deformation and uplift of the Rocky Mountains, Sierra Nevada, Sierra Madre Occidental, and Sierra Madre Oriental (Axelrod & Raven, 1985; Wing, 1987; Graham, 1993). This resulted in cooler and drier climates that precipitated the development of grasslands in central North America (Sanmartín et al., 2001), being thus a third event differentiating the western and the eastern floras. However, Wen (1999) noted that the close biogeographic relationship between western and eastern North America suggests that the Cordilleran range was not an effective barrier to exchange between these two floristic regions.

In the Quaternary period, the flora of North America experienced late Pleistocene full-glacial conditions (20,000–15,000 yr. b.p.), late-glacial climatic amelioration (15,000–10,000 yr. b.p.), and Holocene interglacial conditions of the last 10,000

years (Graham, 1999). The Quaternary can be characterized more by changes in the distributions of plant taxa than by the evolution of new genera and species (Delcourt & Delcourt, 1993). During times of glacial maxima, fragmented populations may have undergone genetic differentiation within isolated refugia. With the onset of interglacial conditions, migration and expansion of distributional ranges would reestablish genetic exchanges between populations within species and among closely related species that were formerly isolated. Grichuk (1984) proposed the term "migration flora" to denote floras that moved into a given region after the preceding flora was eliminated by glacial or periglacial conditions. Delcourt and Delcourt (1993) suggested that the individual elements of such migration floras could move hundred to thousands of kilometers as they differentially responded to changing climatic and competitive conditions. Different groups and species of Onagraceae tribes Epilobieae, Gongylocarpeae, and Onagreae appear to have participated in such Quaternary migrations into western and eastern North America, apparently from areas in the southwestern part of the continent. We hope that this scenario may be tested using other groups of plants and animals, as well as other analytical tools including phylogenetic methods.

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Appendix 1.

North American areas of endemism used in this analysis; see text for sources and explanation. References for plant endemics generally follow Takhtajan (1986); these are supplemented in some areas by Barbour & Christensen (1993), in Canada by Aiken et al. (1999: ⟨www.mun.ca/biology/delta/arcticf/⟩); in California by Hickman (1993), and in Mexico by Rzedowski (1978) and Ramamoorthy et al. (1993). Names were checked against the on-line *Flora of North America* database (⟨http://hua.huh.harvard.edu/FNA⟩). Endemic animals are arranged in the following order: fish, amphibians, reptiles, birds, mammals, invertebrates; within groups, alphabetical by family. References for animal endemics are as follows: [1]Ricketts et al. (1999); [2]*Mammals of the World* (Wilson & Reeder, 1993: ⟨www.nmnh.si.edu/msw/⟩); [3]Avibase (Lepage, 2003: ⟨www.bsc-eoc.org/avibase⟩); [4]*Amphibian Species of the World* (Frost, 2002: ⟨research.amnh.org/herpetology/amphibia/⟩); [5]*Walker's Mammals of the World* (Nowak, 1997: ⟨www.press.jhu.edu/books/walkers_mammals_of_the_world/⟩); [6]*Fishbase* (Froese & Pauly, 2003: ⟨www.fishbase.org⟩); [7]Reptile database (Uetz et al., 2003: ⟨www.reptile-database.org⟩); [8]entomology (California Academy of Sciences, 2003: ⟨www.calacademy.org/research/entomology⟩).

1. *Arctic* (ARC): includes most of coastal Alaska, northern coastal Canada, all of the ice-free Canadian Archipelago, and Greenland. The flora is depauperate in a nearly tree-less region of tundra and polar desert, with fewer than 1000 species of vascular plants. Endemism at the species level is moderate (Aiken et al., 1999), e.g.: Asteraceae: *Taraxacum hyparcticum*; Brassicaceae: *Braya thorild-wulffii*, *Parrya arctica*; Caryophyllaceae: *Cerastium regelii*, *Silene sorensenis*; Orobanchaceae: *Castilleja arctica*; Polemoniaceae: *Phlox richardsonii*. Endemic fauna include Mammals [Cervidae] *Rangifer tarandus pearyi* (Peary caribou)[1,5]; [Leporidae] *Lepus arcticus* (arctic hare)[1,2]; [Soricidae] *Sorex pribilofensis* (Pribiloff Island shrew)[1,5].
2. *Canadian* (CAN): forms a broad band across Canada and Alaska, south of ARC and north of Rocky Mountain (ROC) and Appalachian (APP) regions, including extreme northern New England, Michigan, and Minnesota. Consists primarily of taiga and coniferous boreal forests, with dominant tree species in *Abies*, *Betula*, *Larix*, *Picea*, *Pinus*, and *Populus*. Some endemic plants include Asteraceae: *Aster yukonensis*; Boraginaceae: *Cryptantha shakletteana*; Brassicaceae: *Erysimum aspermum*; Caryophyllaceae: *Silene williamsii*; Fabaceae: *Astragalus ecosmus*; Orobanchaceae: *Castilleja annua*; Polygonaceae: *Eriogonum flavum*; Portulacaceae: *Claytonia bostockii*; Primulaceae: *Douglasia gormanii*. Endemic fauna include Mammals: [Soricidae] *Sorex gaspensis* (Gaspe shrew)[2,5]; Insects: [Lepidoptera] *Coenonympha nepisiquit* (maritime ringlet butterfly)[1].
3. *Appalachian* (APP): includes a small part of southern Ontario and Quebec, Canada, and most of the eastern United States, excluding the Atlantic and Gulf Coastal region (ATL) to the south. Extends from central Maine, southern Canada, and Minnesota to central Georgia, central Alabama, the Ozark Plateau and the Quachita Mts. in Missouri and Arkansas, and eastern Texas. In Texas, corresponds to the "Post Oak Savannah" and "Blackland Prairies" areas of Correll and Johnston (1970). Dominant climax vegetation is the eastern deciduous forest, with dominant tree species in *Acer*, *Aesculus*, *Betula*, *Fagus*, *Magnolia*, *Quercus*, and *Tilia*. Many endemic plant species, including Magnoliaceae: *Magnolia fraseri*; Menispermaceae: *Menispermum canadense*; Pinaceae: *Abies fraseri*; Ranunculaceae: *Aconitum reclinatum*, *Anemone acutiloba*; Rosaceae: *Prunus alleghanensis*; Ulmaceae: *Ulmus serotina*. Endemic fauna include Amphibians: [Plethodontidae] *Desmognathus welten* (Black Mountain salamander)[1,4]; Reptiles: [Emydidae] *Clemmys muhlenbergii* (bog turtle)[1]; Birds: [Emberizidae] *Dendroica kirtlandii* (Kirkland's warbler)[1,3]; Annelids: [Acanthodrilidae] *Diplocardia meansi* (earthworm)[1].
4. *Atlantic and Gulf Coastal* (ATL): occupies the geologic coastal plain of the Atlantic and Gulf Coast states of the United States, from Massachusetts and New Jersey to Florida and west to south-central Texas. In Texas, corresponds to the "Pineywoods" and "Gulf Prairies and Marshes" areas of Correll and Johnston (1970). Also extends across the lower Mississippi River valley to southern Missouri and Illinois. Much of the coastal plain is characterized by extensive forests of *Pinus*, replaced in some areas by *Carya*, *Fagus*, and/or *Quercus*, and in wetter areas by *Taxodium distichum* and species of *Nyssa* and *Fraxinus*. Endemic taxa include Onagraceae (tribe Jussiaeeae): *Ludwigia lanceolata*, *L. pilosa*, *L. ravenii*, and *L. suffruticosa*, and several hundred species including Annonaceae: *Asimina incana*; Iridaceae: *Iris hexagona*; Lauraceae: *Persea palustris*; Pinaceae: *Pinus elliottii*; Salicaceae: *Salix floridana*; Simaroubaceae: *Leitneria floridana*; Taxaceae: *Taxus floridana*, *Torreya taxifolia*. Endemic fauna include Reptiles [Testudinidae] *Gopherus polyphemus* (gopher tortoise)[1]; Birds: [Corvidae] *Aphelocoma coerulescens coerulescens* (Florida scrub jay)[1,3]; [Picidae] *Picoides borealis*

(red-cockaded woodpecker)[1,3]; Mammals: [Ursidae] *Ursus americanus floridanus* (Florida black bear)[5].

5. *North American Prairies* (NAP): includes prairies and plains between the eastern deciduous forest of APP on the east, the coniferous forests of ROC on the west and CAN on the north, and the arid semi-deserts of CHI and TAM to the southwest. Corresponds for the most part with the "Great Plains" (Great Plains Flora Assoc., 1986), but in Texas also includes the "Edwards Plateau," "Rolling Plains," and "High Plains" areas of Correll and Johnston (1970). Grasses are dominant in this region, with a rich mix of perennial forbs, and forest trees in some areas near rivers. No endemic families, few endemic genera, and some endemic species, including the bryophyte Pottiaceae: *Aschisma kansanum*; and Agavaceae: *Yucca rupicola*; Brassicaceae: *Lesquerella angustifolia*; Fabaceae: *Astragalus gracilis*, *Psoralea cuspidata*; Polygonaceae: *Eriogonum correllii*; Valerianaceae: *Valeriana texana*. Endemic fauna include Amphibians: [Plethodontidae] *Typhlomolge (Eurycea) rathbuni* (Texas blind salamander)[1,4] and *T. robusta* (Blanco blind salamander)[1,4]; Birds: [Phasianidae] *Tympanuchus cupido* (greater prairie chicken)[1,3]; Mammals: [Canidae] *Vulpes velox* (swift fox)[1,2].
6. *Vancouverian* (VAN): extends as a coastal strip from Kodiak Island in Alaska to coastal British Columbia, widening in Washington and Oregon to include the Cascade, Olympic, and Coast Ranges, extending into California through the Klamath and Northern Coast ranges in the west and through the southern Cascades into the Sierra Nevada to its terminus in southern California. In California, VAN corresponds to the NW, CW, CaR, and SN regions of *The Jepson Manual* (Hickman, 1993). Conifers dominate the climax vegetation, along with some broad-leaved species of *Acer*, *Alnus*, *Cornus*, *Fraxinus*, *Populus*, and *Quercus*. There are endemic genera and some 500 to 600 endemic species, including Apiaceae: *Lomatium bradshawii*; Asteraceae: *Aster paludicola*, *Erigeron cervinus*, *Senecio clarkianus*; Iridaceae: *Iris bracteata*; Sarraceniaceae: *Darlingtonia californica*; Taxodiaceae: *Sequoia sempervirens*, *Sequoiadendron giganteum*. Endemic fauna include Fishes: [Catostomidae] *Catostomus rimiculus* (Jenny Creek sucker)[1,6]; [Cyprinidae] *Gila bicolor bicolor* (Tui chub)[1,6]; Amphibians: [Dicamptodontidae] *Dicamptodon ensatus* (Pacific giant salamander)[1,4]; Birds: [Strigidae] *Strix occidentalis caurina* (northern spotted owl)[1,3]; Insects: [Lepidoptera] *Colias behrii* (Sierra sulfur butterfly)[1].
7. *Rocky Mountain* (ROC): includes the Rocky Mountains and associated inland ranges from northern British Columbia and southwestern Yukon to central Oregon, south-central Idaho, extreme northeastern Utah, and north-central New Mexico, bounded on the west by VAN and GBA and on the east by CAN and NAP. In the extreme south, ROC borders the deserts of CHI. Also includes some associated outlier ranges, especially extending to the east and south of the main cordillera. Vegetation is zoned vertically, with *Pinus ponderosa* dominant in the lowest zones, and species of *Abies*, *Juniperus*, *Picea*, *Pinus*, *Populus*, and *Pseudotsuga* dominant at higher zones. Some endemic plant species include Apiaceae: *Angelica ampla*, *Lomatium tuberosum*; Brassicaceae: *Draba grayana*; Fabaceae: *Astragalus arrectus*; Orobanchaceae: *Castilleja christii*; Plantaginaceae: *Penstemon elegantulus*; Polemoniaceae: *Phlox colubrina*. Endemic fauna include Fishes: [Cyprinidae] *Gila cypha* (humpback chub)[1,6]; [Salmonidae] *Oncorhynchus clarki lewisi* (westslope cutthroat trout)[1,6]; Mammals: [Mustelidae] *Mustela negripes* (black-footed ferret)[1,2,5]; [Sciuridae] *Cynomys leucurus* (white-tailed prairie dog)[1,2].
8. *Great Basin* (GBA): bounded on the west by the Cascade-Sierra Nevada axis (VAN), on the east by ROC, and on the south by the desert regions of MOJ, SON, and CHI. In California, the boundaries correspond to those of the MP and SNE (including the White and Inyo Mountains) regions of *The Jepson Manual* (Hickman, 1993). Includes the Snake River Plains of southern Idaho and most of the Colorado Plateau, and consists of many north-south trending mountain ranges separated by broad, alkaline basins without external drainage, with much of the area above 1300 m. Characterized by diversity of species of *Artemisia*, Chenopodiaceae, and at higher elevations by some combination of species of *Acer*, *Populus*, *Quercus*, *Juniperus*, and *Pinus*. The region has numerous endemic species, including Asteraceae: *Chaetadelpha wheeleri*, *Erigeron mancus*; Loasaceae: *Mentzelia packardiae*; Papaveraceae: *Canbya aurea*; Plantaginaceae: *Penstemon compactus*; Primulaceae: *Primula maguirei*. Endemic fauna include Fishes: [Cyprinidae] *Ptychocheilus lucius* (Colorado pikeminnow)[1,6]; Mammals [Heteromyidae] *Microdipodops pallidus* (pale kangaroo mouse)[1,2].
9. *Californian* (CAL): occupies a large part of the state of California, including the Central Valley, the Coast Ranges from the San Francisco region south into northwestern Baja California Norte, Mexico, and the Transverse Ranges of southern California. Bounded on the northwest, north, and east by VAN, and on the southeast by MOJ and SON (Raven & Axelrod, 1978). Corresponds to the GV, CW, and SW regions of *The Jepson Manual* (Hickman, 1993). The vegetation varies altitudinally, from treeless grassland in lower areas to chapparal and mixed forests of *Aesculus*, *Platanus*, *Populus*, *Quercus*, *Salix*, and conifers at higher levels. Numerous endemic plant genera and species include Asteraceae: *Erigeron sanctarum*; Fagaceae: *Quercus douglasii*; Ophioglossaceae: *Ophioglossum californicum*; Papaveraceae: the genus *Romneya*; Polygonaceae: the genus *Hollisteria*. Endemic fauna include Fishes: [Cyprinidae] *Gilia bicolor mojavensis* (Mohave Tui chub)[1,6]; Reptiles: [Colubridae] *Masticophis flagellum ruddocki* (San Joaquin whipsnake)[1,7]; Mammals: [Canidae] *Urocyon littoralis* (Island gray fox)[1,2]; [Heteromyidae] *Dipodomys ingens* (giant kangaroo rat)[1,2], *D. venustus* (narrow-faced kangaroo rat)[1,2]; *Perognathus inornatus* (San Joaquin pocket mouse)[1,2]; Insects [Lepidoptera, Pieridae] *Euphydryas editha quino* (Quino checkerspot butterfly)[1].
10. *Mojavean* (MOJ): small but complex region borders VAN and CAL on west, GBA on north, and SON on south and east. Includes Death Valley, adjacent desert ranges, and large desert region of southeastern California, to base of Transverse ranges, corresponding to DMoj region of *The Jepson Manual* (Hickman, 1993). Extends to east through southern Nevada and northwestern Arizona to extreme southwestern Utah (MacMahon, 2000). Predominately shrubby desert dominated by endemic Joshua-tree *Yucca brevifolia* (Agavaceae), with saltbush (*Atriplex*) scrub characteristic of alkaline basins. Other characteristic species

include Agavaceae: *Yucca schidigera*; Asteraceae: *Ambrosia dumosa*; Cactaceae: *Echinocactus polycephalus*, *Ferocactus acanthoides*; and Zygophyllaceae: *Larrea divaricata* subsp. *tridentata*. Some endemic plants include Agavaceae: *Yucca brevifolia*; Asteraceae: *Amphipappus fremontii*; Caryophyllaceae: *Scopulophila rixfordii*; Cactaceae: *Opuntia chlorotica*; Plantaginaceae: *Penstemon calcareus*; Polygonaceae: *Gilmania luteola*. Endemic fauna include Reptiles: [Phrynosomatidae] *Uma scoparia* (Mojave fringe-toed lizard)[1,3]; Mammals: [Muridae] *Microtus californicus scirpensis* (Amargosa vole)[1]; [Sciuridae] *Spermophilus moharensis* (Mojave ground squirrel)[1,2]; Insects: [Orthoptera, Stenopelmatidae] *Ammopelmatus kelsoensis* (Kelso Dunes jerusalem cricket)[1,8].

11. *Sonoran* (SON): ranges from the southern border of the MOJ in southeastern California, south throughout Baja California, Mexico, east through most of southwestern Arizona, and southeast through Sonora, Mexico. Very characteristic plants of the region include columnar cacti such as *Carnegiea gigantea* (saguaro) and *Pachycereus pringlei* (Cactaceae), trees such as *Yucca valida* (Agavaceae), *Cercidium floridum*, and *C. microphyllum* (Cercidiphyllaceae), and shrubs such as *Acacia greggii* (Fabaceae), *Krameria grayi* (Krameriaceae), and *Larrea divaricata* subsp. *tridentata* (Zygophyllaceae). Endemic plant taxa include Onagraceae (tribe Lopezieae): *Lopezia clavata*, and species in various other families, including Agavaceae: *Agave aurea*; Cactaceae: *Opuntia rosarica*; Fabaceae: *Acacia brandegeana*, *A. goldmanii*, *Errazurizia benthami*; Fouquieriaceae: *Fouquieria columnaris*; Lamiaceae: *Hyptis laniflora*; Sapindaceae: *Aesculus parryi*; Sapotaceae: *Sideroxylon peninsulare*. Endemic fauna include Birds: [Emberizidae] *Aimophila carpalis* (rufous-winged sparrow)[1,3]; [Hydrobatidae] *Oceanodroma macarodactyla* (Guadalupe storm petrol, possibly extinct)[1,3]; Insects: [Coleoptera, Carabidae] *Calathus peropacus* (ground beetle; Liebherr, 1991b), *Pelmatellus parallelus* (ground beetle)[1,8]; [Hymenoptera, Anthophoridae] *Agapanthinus* (digger bees; Ayala et al., 1993).
12. *Chihuahuan* (CHI): borders SON and SMO on west, GBA and ROC on north, NAP and TAM on east, and MAS on south. Extends from eastern Arizona and central New Mexico through trans-Pecos Texas and south into Mexico, including most of Chihuahua and Coahuila, eastern Durango, and northern Zacatecas. Cooler desert than the Sonoran Desert, dominated by shrubby *Larrea divaricata* subsp. *tridentata* and species of *Acacia*, *Agave*, *Dalea*, *Ephedra*, *Flourensia*, *Fouqueria*, and *Jatropha*, among others. Trees, mainly species of *Yucca* and *Opuntia*, are found only along larger streambeds. Endemic plant species include Asteraceae: *Ambrosia johnstoniorum*, *Flaveria anomala*, *Gaillardia gypsophila*; Chenopodiaceae: *Meiomeria stellata*; Fabaceae: *Dalea filiciformis*; Hydrophyllaceae: *Phacelia gypsogenia*. Endemic fauna include Fishes: [Cyprinidae] *Campostoma ornatum* (Mexican stoneroller)[1,6], *Notropis chihuahua* (Chihuahua shiner)[1,6]; Reptiles: [Teiidae] *Cnemidophorus tigris variolosus*)[1,7]; Insects [Coleoptera, Carabidae] *Agonum extimum* (ground beetle; Liebherr, 1991a).
13. *Tamaulipan* (TAM): ranges from southeastern Texas to western Coahuila and most of Nuevo León and Tamaulipas in Mexico, excluding southern parts of these states. Bounded on west by CHI and SMR and on north in southern Texas by complex interface with NAP, APP, and ATL. In Texas, corresponds to "South Texas Plains" area of Correll and Johnston (1970). Characterized mostly by thornscrubs or mesquite-grasslands, moister than CHI desert to the west. Vegetation is largely open shrub- and grasslands with *Acacia*, *Aloysia*, *Celtis*, *Condalia*, *Prosopis*, *Ziziphus*, and other spiny species. Endemic plant species include Boraginaceae: *Heliotropium torreyi*; Ebenaceae: *Diospyros palmeri*; Euphorbiaceae: *Croton torreyanus*; Fabaceae: *Acacia rigidula*, *Mimosa malacophylla*; Lauraceae: *Phoebe tampicensis*; Lentibulariaceae: *Pinguicula gracilis*; Plantaginaceae: *Leucophyllum frutescens*; Polygalaceae: *Polygala glandulosa*; Rhamnaceae: *Condalia hookeri*; Rutaceae: *Amyris cordata*. Endemic fauna include Fishes: [Cichlidae] *Cichlasoma cyanoguttatum* (Rio Grande cichlid)[1,6]; Mammals: [Sciuridae] *Cynomys mexicanus* (Mexican prairie dog; Fa & Morales, 1993)[2]; [Talpidae] *Scalopus montanus* (Coahuila mole)[1]; Insects: [Coleoptera, Carabidae] *Platynus bacatellus* (ground beetle; Liebherr, 1992).
14. *Sierra Madre Occidental* (SMO): borders SON and a coastal strip of the Central American Neotropical area (NE) on west, and CHI, the Altiplano of central Mexico (MAS), and the Trans-Mexico Volcanic (TMV) regions on the east and south. Starts near U.S.–Mexico border and extends southeast through western Chihuahua, Durango, a small part of Zacatecas, eastern Sinaloa and Nayarit, to central Jalisco. The main cordillera consists of an extensive volcanic terrain from 200 to 2200 m, with a pronounced eastern tilt. The region is characterized by a variety of habitats including both dry and subtropical forests at lower elevations, dry mixed forests at mid-elevations, and pine/oak forests above 2000 m. Endemic plants include Onagraceae (tribe Lopezieae): *Lopezia ciliatula*, *L. conjugens*, *L. gentry*, *L. laciniata*, *L. lopezioides*, *L. orata*, *L. semeiandra*, *L. sinaloensis*, and *L. suffrutescens*, and species in various other families, including Asteraceae: *Alvordia congesta*, *Hofmeisteria sinaloensis*, *Perityle grandifolia*; Cactaceae: *Ferocactus schwarzii*, *Mamillaria rubidea*, *Stenocereus martinezii*; Crassulaceae: *Echeveria kimnachii*, *Sedum copalense*; Ericaceae: *Arbutus madrensis*; Euphorbiaceae: *Ditaxis sinaloae*; Polygonaceae: *Ruprechtia occidentalis*. Endemic fauna include Birds: [Picidae] *Campephilus imperialis* (imperial woodpecker)[1,3]; Insects: [Coleoptera, Carabidae] *Elliptoleus olisthopoides* (ground beetle; Liebherr, 1991a); [Neuroptera, Myrmeleontidae] *Marcandula apicalis* (antlion)[8].
15. *Trans-Mexican Volcanic Belt* (TMV): extends in narrow, slightly northwest to southeast band in central Mexico, from central Jalisco and Guerrero through southern Estado Mexico barely to Puebla. Borders SMO and the coastal NE strip on west and south, MAS on north, and a transitional montane area between SMR and SMS on east. Major volcanic peaks (3900–4000 m) covered by *Pinus hartwegii* and coarse bunchgrasses *Festuca tolucensis*, *Calamagrostis tolucensis*, and *Muhlenbergia quadridentata*. Other characteristic taxa included species of *Achillea*, *Alchemilla*, *Arenaria*, *Cerastium*, *Geranium*, *Ranunculus*, and *Trifolium*. Among the very large number of endemic plant species are Onagraceae (tribe Lopezieae): *Lopezia longiflora*; at least seven endemic alpine species of Asteraceae: *Cirsium nivale*, *Gnaphalium sarmentosum*, *G. vulcanicum*, *Senecio calcarius*,

S. gerberaefolius, *S. procumbens*, and *S. roseus*; and many other taxa, including Garryaceae: *Garrya longifolia*; Meliaceae: *Cedrela saxatilis*; Orchidaceae: *Pleurothallis nigriflora*; Oxalidaceae: *Oxalis stolonifera*, *O. cuernavacana*. Endemic fauna include Amphibians: [Ambystomidae] *Ambystoma* (*Rhyacosiredon*) *rivularis* (Michoacán stream salamander)[4]; Mammals: [Muridae] *Neotomodon altstoni* (Mexican volcano mouse)[2], *Reithrodontomys chrysopsis* (volcano harvest mouse)[2]; Insects: [Coleoptera, Carabidae] *Calathus azteca*, *Elliptoleus corvus*, *E. luteipes* (ground beetles; Liebherr, 1991b), *Platynus machetellus* (ground beetle; Liebherr, 1992); [Hymenoptera, Anthophoridae] *Loxoptilus* (digger bees; Ayala et al., 1993).

16. *Mexican Altiplano* (MAS): in central Mexico lies between CHI on north, the mountains of SMO on the west and SMR on the east, and TMV on the south. Includes central and southern Zacatecas, southeastern Durango, eastern Jalisco and Michoacán, northern Estado México, western San Luis Potosí and Hidalgo, the Federal District, Aguascalientes, Guanajuato, and Querétaro. This region is characterized by mixed, less xeromorphic tree communities of *Acacia*, *Ipomoea*, and *Opuntia*. Endemic plant species include Agavaceae: *Yucca queretaroensis*; Asteraceae: *Acourtia elizabethiae*; Berberidaceae: *Berberis albicans*; Cactaceae: *Lophophora diffusa*, *Mammillaria camptotricha*; Fabaceae: *Acacia sororia*; Lentibulariaceae: *Pinguicula agnata*. Endemic fauna include Insects: [Coleoptera, Carabidae] *Agonum suturale* (ground beetles; Liebherr, 1991a); [Hymenoptera, Halictidae] *Paragapostemon* (halictic bees; Ayala et al., 1993).
17. *Sierra Madre Oriental* (SMR): borders CHI and MAS on west and TAM on east, including parts of southern Coahuila and Nuevo León, eastern Zacatecas, San Luis Potosí and Hidalgo, most of Tlaxcala, western Puebla, and a small part of western Veracruz and southwestern Tamaulipas. A geologically complex montane area with high levels of endemism in the relatively moist eastern part; lower elevations in the southeast support tropical evergreen forest. At middle to higher elevations (1000–2000 m), strips of warm-temperate to subtropical mesophytic forest occur, with deciduous/semi-evergreen species. Pine and/or oak forest occur at highest elevations. The mixed forest contains genera characteristic of the Appalachian region, such as *Carpinus*, *Cornus*, *Fagus*, *Hamamelis*, *Liquidambar*, *Pinus*, *Platanus*, and *Quercus*, as well as more typically tropical elements, like *Eugenia*, *Meliosma*, *Rapanea*, and *Turpinia*. Among the very large number of endemic plants are Onagraceae (tribe Lopezieae): *Lopezia nuevoleonis*; and many other taxa, including Caprifoliaceae: *Viburnum cuneifolium*; Celastraceae: *Wimmeria concolor*; Clethraceae: *Clethra pringlei*; Crossosomataceae: *Velascoa*; Fagaceae: *Fagus mexicana*, *Quercus germana*, *Q. rysophylla*; Juglandaceae: *Juglans mollis*; Oleaceae: *Forestiera racemosa*; Sabiaceae: *Meliosma alba*. Endemic fauna include Reptiles: [Anguidae] *Abronia graminea* (terrestrial arboreal alligator lizard)[7], *A. taeniata* (bromeliad arboreal alligator lizard)[7]; Insects [Coleoptera, Carabidae] *Calathus rotgeri*, *C. potosi* (ground beetles; Liebherr, 1991b), *Platynus robustulus* (ground beetle; Liebherr, 1992); [Lepidoptera, Papilionidae; Llorente-Bousquets & Luis-Martínez, 1993] *Parides alexiares* (Oaxacan swallowtail), *Priamides erostratinus* (swallowtail), *Protesilaus epidaus tepicus* (swallowtail).
18. *Sierra Madre del Sur* (SMS): east-west oriented mountain area, ranging from 1200 to 3500 m, including eastern Guerrero, northwestern Oaxaca, and southern Puebla and Morelos. Connects to north with TMV, MAS, and SMR, but mostly surrounded by lowland NE, and as such is southernmost part of the Madrean Region (Takhtajan, 1986). Includes mesic habitats with temperate evergreen forests and woodlands. The diversity of these woodlands is very high, including species of *Quercus* and *Juniperus*, as well as genera of more southern, tropical derivation. Endemic plants include Onagraceae: (tribe Fuchsieae) *Fuchsia ravenii* and (tribe Lopezieae): *Lopezia smithii*, as well as Agavaceae: *Yucca mixtecana*; Lauraceae: *Mocinnodaphne cinnamomoidea*; Malvaceae: *Hibiscus tenorii*; Melastomataceae: *Miconia teotepecensis*; Ruscaceae: *Maianthemum amoenum*, *M. macrophyllum*, *M. comaltepecense*. Endemic fauna include Amphibians: [Plethodontidae] *Thorius grandis* (grand minute salamander), *T. infernalis* (Atoyac minute salamander); Reptiles: [Anguidae] *Abronia deppii* (alligator lizard); Insects: [Coleoptera, Carabidae] *Calathus ovipennis*, *Elliptoleus crepericornis*, *E. whiteheadi* (ground beetles; Liebherr, 1991b), *Platynus platynellus* (ground beetle; Liebherr, 1992).
19. *Neotropical* (NE): large region, essentially the Neotropical Kingdom of Takhtajan (1986), comprises everything south of the Madrean and North American regions. For purposes of this analysis, NE includes a broad spectrum of tropical sub-regions, from the southernmost, tropical part of the Florida Peninsula through the islands of the Caribbean region, most of the coastal plains of Mexico, and all of Central America to most of South America. Among the very large number of endemic plant taxa are Onagraceae, tribe Hauyeae and numerous species of *Fuchsia* (tribe Fuchsieae) and *Ludwigia* (tribe Jussieeae), and the plant families Brunelliaceae, Cyclanthaceae, Desfontainiaceae, and Marcgraviaceae. Endemic fauna include Amphibians: [Hylidae] *Gastrotheca* (*Notodelphis*) *ovifera* (giant marsupial frog)[4]; Reptiles: [Boidae] subfamily Boinae (boas and constrictors)[7]; Birds: family Rheidae (rheas)[3]; Mammals[2,5]: [Camelidae] *Lama* (alpacas, guanacos, llamas); family Caviidae (cavies, guinea pigs); family Chinchillidae (chinchillas and viscachas); [marsupials, Microbiotheriidae] *Dromiciops* (monitos del monte).
20. *East Palearctic* (EP): defined here to include the northeast Asian parts of the Circumboreal Region and essentially all of the diverse Eastern Asiatic Region of Takhtajan (1986), including the eastern Himalayas, most of China, the Korean Peninsula, Japan and the north Pacific Ocean island series. The flora of this region is enormous and very rich in endemics, including in Onagraceae several species of *Circaea* (tribe Circaeeae; Boufford, 1982) and *Epilobium* (tribe Epilobieae; Chen et al., 1992), as well as the endemic families Cephalotaxaceae, Ginkgoaceae, and Trochodendraceae, and more than 300 endemic genera [e.g., Apiaceae: *Tetrapanax*; Berberidaceae: *Nandina*; Cornaceae: *Aucuba*; Lardizabalaceae: *Akebia*; Rosaceae: *Chaenomeles*; Rutaceae: *Poncirus*; Taxodiaceae: *Cryptomeria*]. Endemic fauna include Fishes: [Siluridae] *Silurus asotus* (Amur catfish)[6]; Reptiles–Crocodilians: family Gavialidae (gharial)[7]; Birds [Phasianidae] *Gal-*

lus gallus (red jungle fowl, chicken)[4]; Mammals[2,5]: order Dermoptera (flying lemurs); family Hylobatidae (gibbons and lesser apes); [Leporidae] *Pentalagus* (Ryukyu rabbit).

21. *West Palearctic* (WP): defined here to include European and west Asian parts of the Circumboreal Region (Takhtajan, 1986), essentially everything west of EP in Eurasia. The flora includes many endemic plants, including Apiaceae: *Agasyllis, Endressia, Thorella*; Asteraceae: *Berardia*; Boraginaceae: *Megacaryon, Trigonocaryum*; Brassicaceae: *Microstigma, Pseudovesicaria*; Fabaceae: *Petteria*; Gesneriaceae: *Haberlea*). Endemic fauna include Fishes: [Siluridae] *Silurus aristotelis* (Aristotle's catfish)[6]; Amphibians: [Pelobatidae] *Pelobates* (European spadefoot toads)[4]; Mammals: [Bovidae] *Ovis musimon* (mouflon sheep)[2,5].

FLORAL BIOLOGY OF *HESPERANTHA* (IRIDACEAE: CROCOIDEAE): HOW MINOR SHIFTS IN FLORAL PRESENTATION CHANGE THE POLLINATION SYSTEM[1]

Peter Goldblatt,[2] Ingrid Nänni,[3] Peter Bernhardt,[4] and John C. Manning[5]

Abstract

Field observations, floral dissections of a representative range of *Hesperantha* species, and pollen load analyses of insects captured on many of them indicate that flowers of this African genus are cross pollinated by a relatively broad range of insects. The pollination ecology of *Hesperantha* can be divided into four overlapping systems that exploit insects of four orders (Coleoptera, Diptera, Hymenoptera, and Lepidoptera). Species of the *H. falcata* type have erect or nodding, salver-shaped, strongly fragrant, white flowers that open in the mid to late afternoon and evening and are pollinated by long-tongued apid bees and/or noctuid moths. Species of the *H. pauciflora* type have a virtually identical floral morphology, but the perianth is yellow or pink to mauve or blue and the flowers are usually unscented and are open during the day, closing between midday and late afternoon, ca. 16:30 H. Flowers of this type are also pollinated by apid bees, but in the southern African winter-rainfall zone other effective pollinators include nemestrinid flies (*Prosoeca*) with relatively short probosces and hopliine scarab beetles. In *H. latifolia* type flowers the perianth is pink to magenta or red (rarely pale yellow), odorless, opens during the day but has an elongate perianth tube exceeding 18 mm in length. These flowers are pollinated mainly by long-proboscid flies in the genera *Prosoeca* and *Stenobasipteron* (Nemestrinidae) or *Philoliche* (Tabanidae), but the red flowers of *H. coccinea* are pollinated by a guild of large butterflies including *Papilio* and the satyrid *Aeropetes*. Lastly, *H. vaginata* has odorless and nectarless, short-tubed yellow flowers, usually with contrasting dark markings, that open only during the day and are pollinated exclusively by the hopliine scarab beetle, *Clania glentyonensis*. The taxonomic distribution of plant species with these pollination systems makes it clear that shifts in pollination systems have occurred repeatedly across *Hesperantha*, although floral morphology and nectar biochemistry are relatively conservative. Whether flowers are nocturnal, crepuscular, or diurnal, only four variables affect the floral ecology: length of the perianth tube, presence or absence of floral fragrance, timing of anthesis, and the closely associated trait of perianth color. Thus, species with pink, magenta, red, or yellow flowers close at night and are rarely fragrant, whereas those with white or pale yellow flowers are nearly always fragrant and either open late in the day or only at sunset and remain open for most of the night. Species show considerable variation in nectar volume and sugar concentration, closely correlated with pollination system, while two long-tubed species with floral characters typical of long-proboscid fly pollination produce no nectar and are inferred to be Batesian or guild mimics that achieve pollination by deception.

Key words: bees, floral ecology, *Hesperantha*, hopliine beetles, Iridaceae, long-proboscid flies, nectar, pollination systems, settling moths.

The radiation and diversification of the African Iridaceae depend to a greater or lesser extent on the plasticity of pollination mechanisms, and all the larger genera of the family exhibit a wide range of floral adaptations and correlated sets of insect or avian pollinators (Bernhardt & Goldblatt, 2000). For example, *Lapeirousia* is pollinated by long-proboscid flies, or bees and butterflies, or moths (Goldblatt et al., 1995). *Romulea* exploits scarab beetles, pollen-collecting bees or, in at least two species, long-proboscid nemestrinid flies (Goldblatt et al., 1998a; Manning & Goldblatt, 1996, and unpub-

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lished). The majority of species of *Gladiolus* appear to be pollinated primarily by nectar-feeding apid and anthophorine bees (Goldblatt et al., 1998b), but some red-flowered species are pollinated by the large butterfly *Aeropetes* (Johnson & Bond, 1994), while others are dependent on andrenid bees, a combination of bees and hopliine beetles (Goldblatt et al., 1998a), long-proboscid flies, moths, or birds (Goldblatt & Manning, 1998; Goldblatt et al., 1999, 2001).

Hesperantha, a mid-sized genus of subfamily Crocoideae (syn. Ixioideae), comprises approximately 80 species (Goldblatt, 1984, 1986, 1987, 1993, 2003; Hilliard & Burtt, 1986; Goldblatt & Manning, 1996) distributed from the southern tip of Africa through the eastern African mountains as far north as Ethiopia and Cameroon. Diversity is greatest in southern Africa, where there are two centers of diversity and regional endemism: the Drakensberg of South Africa and Lesotho; and the west coast and near interior of Northern Cape and Western Cape Provinces of South Africa. Compared with the approximately 260 species of *Gladiolus*, the 50 species each of *Ixia* or *Watsonia*, or the 40 species of *Lapeirousia*, *Hesperantha* species have a conservative floral morphology. The relatively small flowers (tepals typically 10–25 mm long, exceptionally to 37 mm) are radially symmetric, have subequal tepals, and are arranged in slender to compact spicate inflorescences. The flowers of most species have a symmetrical androecium and a style that diverges at the mouth of the floral tube into three long, spreading branches. Interspecific floral variation is restricted to perianth tube length and degree of curvature, perianth color (uniformly white to cream vs. various shades of pink to purple, or yellow, sometimes with dark markings), the presence or absence of fragrance, the type of floral odor, and the timing of anthesis (Goldblatt, 1984, 2003).

A particularly unusual aspect of floral variation within this genus is the close linking of floral pigmentation with the presence of floral odor and timing of anthesis. White- or cream-flowered species of the southern African winter-rainfall zone are crepuscular or nocturnal and produce a strong floral fragrance, whereas species with flowers of other colors, and the white-flowered species of eastern southern Africa, are typically odorless, at least to the human nose. Field studies of the pollination systems of a selection of *Hesperantha* species were undertaken to define and compare intrageneric trends in the evolution of pollination mechanisms and the function(s) of floral traits.

Materials and Methods

Inflorescence phenology and floral life span

Direct observations are presented on 34 *Hesperantha* species made in the field from 1993 to 2002 (Table 1) and supplemented by living collections at Kirstenbosch Botanic Gardens, Cape Town, and the Missouri Botanical Garden, St. Louis. Observations were made in the southern spring, summer, or autumn at sites in southern Africa (August to April). Observations of insect foraging involved 4 to 10 hours per plant species (or occasionally more) and included recording of floral attractants (pigmentation, scent), rewards (nectar), the mode and timing of anthesis (opening of individual buds), daily phenology, anther dehiscence patterns, expansion of stigmatic lobes, the behavior of insects on the flower, and the taxonomic diversity of floral foragers. Floral scent was noted in the field and in cultivated plants. Scents too weak to be immediately discerned by the human nose were recorded after individual flowers were picked and placed in clean, lidded glass jars and stored in a warm place. The contents of each jar was smelled after a minimum of 60 minutes (Buchmann, 1983). Plant voucher specimens are deposited in the herbaria at the Missouri Botanical Garden (MO) and Kirstenbosch Botanic Gardens (NBG) (Table 1).

Compatibility

Compatibility relationships were examined in two species, *Hesperantha quadrangula* and *H. pallescens*, both maintained in the laboratory and isolated from possible pollinators. Fruit and seed set were compared in five hand-selfed flowers and five flowers crossed with pollen of another individual of the same species. In the Iridaceae hand-selfing of as few as five flowers is usually sufficient, as results are seldom mixed. Either all self crosses result in seed set or none do. Likewise, xenogamous crosses always succeed.

Nectar analysis

Nectar volume measurements were taken primarily from unbagged flowers in the field, soon after they opened, reflecting both rates of secretion and depletion. To collect nectar, mature flowers were picked and nectar was withdrawn from the base of the perianth tube with 3 µl capillary tubes after separating the ovary from the perianth base. The percentage of sucrose equivalents in fresh nectar was measured in the field or laboratory using a Bellingham and Stanley hand-held refractometer (0–

Table 1. Study sites and voucher information for *Hesperantha* species studied. Vouchers are housed at MO (Goldblatt & Manning) or at NBG (other collectors). All study sites are in South Africa.

Species	Study site	Voucher
H. acuta (Lichst. ex Roem. & Schult.) Ker Gawl.	Western Cape, foot of Vanrhyn's Pass	*Goldblatt & Manning 11070*
H. bachmannii Baker	Glenlyon, Nieuwoudtville	*Goldblatt & Nänni 11152*
H. baurii Baker	Free State, The Sentinel	*Goldblatt & Manning 11051*
H. brevicaulis (Baker) G. J. Lewis	Mpumalanga, God's Window	*Goldblatt 72*
H. coccinea (Backh. & Harv.) Goldblatt & J. C. Manning		
site 1	Mpumalanga, near Lunsklip falls	*Goldblatt s.n.* no voucher
site 2	KwaZulu-Natal, Karkloof	*Goldblatt & Nänni 11242*
site 3	KwaZulu-Natal, Highmoor	*Goldblatt & Nänni 11249*
H. cucullata Klatt	Northern Cape, Nieuwoudtville	*Goldblatt 3954*
H. erecta (Baker) Benth. ex Baker	Western Cape, Vredenburg	*Goldblatt & Manning 11084*
H. falcata (L. f.) Ker Gawl.		
site 1	Western Cape, near Darling	*Goldblatt & Nänni 11096*
site 2	Western Cape, Caledon, Drayton	*Goldblatt 11161*
H. fibrosa Baker	Western Cape, Fairfield, Napier	*Goldblatt & Nänni 10251*
H. flava G. J. Lewis	Western Cape, near Matjesfontein	*Goldblatt 6074*
H. flexuosa Klatt	Northern Cape, near Springbok	*Goldblatt & Porter 12086*
H. grandiflora G. J. Lewis	Free State, The Sentinel	*Goldblatt s.n.* no voucher
H. huttonii (Baker) Hilliard & Burtt	Eastern Cape, Kologha Forest	*Goldblatt & Porter 12007*
H. lactea Baker	KwaZulu-Natal, Inchanga	*Goldblatt & Nänni 11235*
H. latifolia (Klatt) M. P. de Vos	Northern Cape, Kamiesberg	*Goldblatt & Manning 9723*
H. leucantha Baker	Free State, The Sentinel	*Goldblatt & Nänni 11232*
H. luticola Goldblatt	Northern Cape, near Middelpos	*Goldblatt 6067*
H. marlothii R. C. Foster	Northern Cape, near Nieuwoudtville	*Goldblatt 11403*
H. oligantha (Diels) Goldblatt	Northern Cape, Hantamsberg	*Goldblatt & Manning 10043*
H. pallescens Goldblatt	Western Cape, Piekeniers Kloof	*Goldblatt & Nänni 11161*
H. pauciflora G. J. Lewis (pink flowers)		
site 1	Northern Cape, Oorlogskloof	*Goldblatt & Manning 9975*
site 2	Northern Cape, near Nieuwoudtville	*Goldblatt s.n.* no voucher
H. pauciflora (yellow flowers)	Northern Cape, Papkuilsfontein south of Nieuwoudtville	*Goldblatt 11102*
H. pilosa (L. f.) Ker Gawl. (blue flowers)	Northern Cape, Bokkeveld Mts.	*Goldblatt 6272*
H. pilosa (white flowers)		
site 1	Western Cape, Darling	*Goldblatt & Nänni 11162*
site 2	Western Cape, Viljoen's Pass	*Goldblatt 11113*
site 3	Western Cape, Rooisand, Bot River	*Goldblatt 11148*
H. pseudopilosa Goldblatt	Northern Cape, near Nieuwoudtville	*Goldblatt 11108*
H. pubinervia Hilliard	Free State, The Sentinel	*Goldblatt & Manning 11052*
H. quadrangula Goldblatt	Northern Cape, near Middelpos	*Goldblatt 11157*
H. radiata (Jacq.) Ker Gawl.		
site 1	Western Cape, Malmesbury	*Goldblatt s.n.* no voucher
site 2	Northern Cape, near Nieuwoudtville	*Goldblatt & Nänni 11104A*
H. rivulicola Goldblatt	Northern Cape, near Nieuwoudtville	*Goldblatt & Nänni 11104*
H. scopulosa Hilliard	Free State, The Sentinel	*Goldblatt & Manning 9856*
H. similis (N. E. Br.) R. C. Foster	Mpumalanga, Long Tom Pass	*Goldblatt & Manning 10480*
H. spicata (Burm. f.) Ker Gawl.	Western Cape, Malmesbury	*Goldblatt 11087B*
H. stenosiphon Goldblatt	Eastern Cape, Cathcart district	*Goldblatt & Porter 12995*
H. sufflava Goldblatt	Western Cape, Malmesbury	*Goldblatt & Nänni 11087*
H. vaginata (Sweet) Goldblatt	Northern Cape, Glenlyon Farm	*Goldblatt 4035*
H. woodii Baker	Eastern Cape, Naude's Nek	*Goldblatt & Manning 11067*

50%) from five or more individuals per population, unless fewer individuals were available. Additional nectar samples were dried on Whatman filter paper no. 1 and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for HPLC nectar sugar analysis.

INSECT OBSERVATION AND POLLEN LOAD ANALYSES

Behavior of insects on *Hesperantha* flowers was carefully observed to see whether insects contacted anthers and stigmas while foraging. Insects observed probing the floral tube or brushing the anthers or stigmas were captured and killed in a jar using ethyl acetate fumes. Pollen was removed from insects after specimens were pinned. To prevent contamination of the body of an insect with pollen carried by another in the same jar, each insect was wrapped in tissue as soon as it was immobilized by jar fumes. Body length and proboscis length of insects was recorded from captured specimens. Night-flying moths are difficult to capture simply because darkness makes them difficult to locate. Use of flashlights covered with translucent red cellophane paper for illumination significantly assisted observation and capture. Capturing some insects (especially long-proboscid flies) at some sites appeared to reduce the population significantly, so we therefore killed as few of these insects as necessary to obtain specimens for identification and pollen load analysis.

Removal of pollen from an insect involved gently scraping pollen off the body with a dissecting needle (see Goldblatt et al., 1998a, b). The residue from needle probes was collected on glass slides and mounted in 1 to 2 drops of Calberla's fluid (Ogden et al., 1974). In the case of long-proboscid flies, which are large insects, sites of pollen deposition are often quite discrete for each plant visited, and pollen species can often be identified without recourse to microscopic examination due to pollen coloration and position. Pollen grains were identified microscopically by comparison with a temporary reference set of pollen grain slides made from plants flowering at study sites. *Hesperantha* pollen grains are distinguished from co-blooming species, other than members of Iridaceae subfamily Crocoideae, by their large size, perforate-scabrate exine, and monosulcate aperture with prominent 2-banded operculum (Goldblatt et al., 1991).

Insect specimens were identified by R. W. Brooks, University of Kansas (Apidae), H. Dombrow, Worms, Germany (Scarabaeidae), D. Kroon, Sasolburg, South Africa, and H. Kruger, Transvaal Museum, Pretoria (Lepidoptera—moths), J. C. Manning (Diptera, Lepidoptera—butterflies), and Kim E. Steiner, National Botanical Institute, Cape Town (Mellittidae, Scarabaeidae). Voucher specimens are deposited at the Snow Entomological Museum, Lawrence, Kansas.

RESULTS

INFLORESCENCE PHENOLOGY AND FLORAL LIFE SPAN

Most *Hesperantha* species have an erect inflorescence reaching a height of 5–30 cm, but a few species of rocky habitats and cliffs, including *H. brevicaulis* and *H. scopulosa*, have weak, drooping stems and a nodding spike (Fig. 1). Individuals produce one or, in some species, two or more, simple spicate inflorescences annually, and flowering is closely synchronized within the same species or population both seasonally and diurnally. Flower buds are arranged more or less helically along the spike (Goldblatt, 1984, 2003). In six species, including *H. flava*, *H. humilis*, and *H. latifolia*, the flowering stem is mostly or entirely subterranean so that the flowers are borne close to ground level (Fig. 1B). Flowering periods broadly subdivide into a spring season (August and September, or October in a few species) in the southern African winter-rainfall zone or a summer–autumn season (December to April) in the summer-rainfall zone (Table 2). This coincides with the period of optimal plant growth during or soon after the main rainy season for the geographical area. A few species of the summer-rainfall zone flower in early to late spring (Hilliard & Burtt, 1986), sometimes before foliage leaves have been produced, but for logistical reasons we did not study these early flowering species.

The pattern of flower buds opening on an inflorescence is acropetal. In all *Hesperantha* species a mature flower expands and closes again within 12 hours at specific times characteristic of the species or population. White, cream, or pale yellow flowers of the southern African winter-rainfall zone are fragrant (Table 2) and typically open in the mid to late afternoon or at sunset and close at specific times in the night, always before daylight (Table 3). Flowers of other colors, and white- to cream-flowered species of the summer-rainfall zone, are scentless (Table 2) and open either in the early morning (*H. ciliolata*, *H. pilosa* blue-flowered form, as well as most pink-flowered species of eastern southern Africa) and close soon after midday, or open after the middle of the day (*H. pauciflora*) and close before sunset (Table 3). The red flowers of *H. coccinea* open in the early morning and close shortly before sunset. Examples of perianth color and form, re-

Table 2. Floral characteristics of *Hesperantha* species arranged according to flower type. Measurements of the perianth tube include the wider upper portion that accommodates the head of a long-tongued insect; + = presence, − = absence, trace = amount too little to measure volumetrically; salver = salverform. White-flowered populations of *H. falcata* and *H. pilosa* are listed in the first group, while yellow-flowered or blue-flowered populations respectively are included in the second group. Examples of flower color in *Hesperantha* species are available in Manning et al. (2002) and at http://www.mobot.org/MOBOT/Research/Hesperanthapollination.pdf.

Species	Flower shape	Flower color	Tube length mm	Scent	Nectar	Flowering time
***Hesperantha falcata* group**						
H. acuta	salver	white	8–11	yes	+	Aug.–Sep.
H. bachmannii	nodding tube	white	8–10	yes	+	Aug.–Sep.
H. cucullata	salver	white	7–9	yes	+	Aug.–Sep.
H. erecta	salver	white	8–10	yes	+	July–Sep.
H. falcata (also see below)	salver	white	7–9	yes	+	Aug.–Sep.
H. flava	tube-salver	yellow	20–26	yes	+	June–July
H. flexuosa	salver	white	7–9	yes	+	Aug.–Sep.
H. marlothii	nodding tube	white	ca. 12	yes	+	July–Aug.
H. pilosa (also see below)	salver	white	9–10	yes	+	Aug.–Sep.
H. pseudopilosa	salver	white	8–10	yes	+	Aug.–Sep.
H. quadrangula	salver	white	ca. 3	yes	trace	Sep.
H. radiata	nodding tube	white to cream	10–12	yes	+	Aug.–Sep.
H. rivulicola	salver	white	9–11	yes	+	Aug.–Sep.
H. spicata	salver	white	4–5	yes	+	Aug.–Oct.
H. sufflava	salver	yellow	12–16	yes	+	July–Aug.
***Hesperantha pauciflora* group**						
H. baurii	salver	pink	8–10	no	trace	Jan.–Feb.
H. ciliolata	salver	pink	4–5	yes	+	Sep.
H. falcata (also see above)	salver	yellow	7–8	no	?	Aug.–Sep.
H. fibrosa	salver	pink	7–9	no	+	Aug.–Sep.
H. humilis	tube-salver	pink	18–22	no	−	June–July
H. leucantha	salver	pale pink	10–15	no	+	Jan.–Feb.
H. lactea	salver	creamy yellow	7–8	no	+	Jan.–Feb.
H. luticola	tube-salver	white with large dark marks on the tepals	30–45	no	trace	July–Aug.
H. pauciflora	salver	pink to purple, or yellow	6–8	no	trace or +	Aug.–Sep.
H. pilosa (also see above)	salver	blue	7–9	no	+	Aug.–Sep.
H. similis	salver	pink	4–5	no	trace	Jan.–Feb.
***Hesperantha latifolia* group**						
H. brevicaulis	tube-salver	pink	22–30	no	+	Mar.–Apr.
H. coccinea	tube-salver	red (or pink)	(25–)30–38	no	+	Dec.–May
H. grandiflora	tube-salver	pink, anthers brown	28–32	no	+	Jan.–Feb.
H. huttonii	tube-salver	pale pink	22–35	no	+	Feb.–Mar.
H. latifolia	tube-salver	purple	20–27	no	+	Aug.–Sep.
H. oligantha	tube-salver	purple	25–35	no	+	Sep.
H. pubinervia	tube-salver	salmon-pink	20–25	no	−	Jan.–Feb.
H. scopulosa	tube-salver	pink	32–42	no	−	Feb.–Mar.
H. stenosiphon	tube-salver	pink, anthers black	45–60	no	+	Feb.–Mar.
H. woodii	tube-salver	pink	33–40	no	+	Feb.–Mar.
***Hesperantha vaginata* group**						
H. vaginata	cup	yellow with brown markings	5–7	no	−	Aug.–Sep.
Unplaced species						
H. pallescens	tube-salver	pale yellow	18–22	no	+	Sep.

Table 3. Contrasted timing of floral opening and closing in selected *Hesperantha* species. Only species for which precise information is available are included, and data are for study populations only (as in Table 1). Timing varies within populations according to weather conditions, and other populations of the same species may have different opening and closing patterns. Flowers of *H. scopulosa* do not fully close and have the tepals fully expanded for all daylight hours and partially so at night. N/a = not assessed.

Species	Opening	Closing	Days open
	White-, cream-, or pale yellow-flowered species		
H. bachmannii	16:00–16:30	6:30–7:00	4
H. cucullata	(15:00–)16:00–16:30	(19:00–)20:00–20:30	n/a
H. erecta	(14:00–)15:00–15:30	(17:00–)18:30–19:00	4–5
H. falcata	(12:30–)15:30–16:30 or 17:30–18:00	21:00–21:30 or after 2:00	4–5
H. flava	16:00–17:00	n/a	n/a
H. lactea	11:45–12:30	16:00–16:30	n/a
H. marlothii	17:00–17:30	4:00–4:30	n/a
H. pallescens	8:00–8:30	18:30–19:00	n/a
H. pilosa (white-flowered)	17:30–18:00	3:30–4:30	4
H. pseudopilosa	(15:00–)18:00–18:30	after 0:00	n/a
H. quadrangula	16:00–16:30	19:00–19:30	3–4
H. radiata	18:00–18:30	5:30–6:30	6–7
sample 2	17:00–17:30	5:30–6:00	n/a
H. rivulicola	16:15–16:45	after 0:00	n/a
H. spicata	18:00–18:30	0:00–0:30	4–5
H. sufflava	15:30–16:00	after 0:30	4–5
	Pink-, blue-, or deep yellow-flowered species		
H. baurii	7:30–8:00 or 11:00–11:30	11:30–12:00 or 16:30–17:00	3–4
H. brevicaulis	ca. 11:00	n/a	n/a
H. coccinea	7:30–8:00	18:00–19:00	3–4
H. humilis	8:00–9:00	16:00–16:30	n/a
H. oligantha	n/a	14:00–14:30	n/a
H. pauciflora	(13:00–)14:00–14:30	17:00–17:30	n/a
H. pilosa (blue-flowered)	8:30–9:00	12:30–13:00	n/a
H. vaginata	14:30–15:00	16:30–17:00	n/a
H. woodii	9:00–9:30	14:00–14:30	n/a

produced in color, are available in Manning et al. (2002). Representative photographs of *Hesperantha* flowers are also posted at the following URL together with this article: http://www.mobot.org/MOBOT/Research/Hesperanthapollination.pdf.

A flower typically lasts four days before collapse of the perianth, but in a few species with a white perianth, flowers last six or seven days (e.g., *Hesperantha radiata*, *H. spicata*), yet maintain the pattern of opening and closing at specific times (Table 3). Flower buds on the same inflorescence open sequentially, usually one day apart; hence, there may be three or four flowers open at any time on an inflorescence for species with flowers lasting four days, but up to eight flowers open in species in which flowers last six or seven days. When flowers close, the tepals cloak the anthers and stigmas completely. Ambient temperature influences anthesis. On cold (< 15°C), heavily overcast, or misty days, flowers may not open completely for the entire day or the normal timing of opening may be delayed until conditions are more favorable. The only exception we have encountered is *H. scopulosa*, the flowers of which do not close completely, but the tepals half close at sunset, and re-open fully to become extended at 90° to the tube after 7:00 H the next morning.

Flowers of all species studied are weakly protandrous. The anthers dehisce longitudinally within one to three hours after the tepals of a new bud first unfold, but this depends to some extent on ambient temperature and humidity (see above) and anthers dehisce later in the day under wet-cool conditions. The three stylar arms, the adaxial surfaces of which comprise the stigmatic surfaces, are held erect when the flower first opens but they diverge later during the same day, in most species spreading outward below the erect or divergent an-

thers, coming to lie over the extended tepals. In all species the style divides at (or in a few species below) the mouth of the perianth tube into three long, slender arms (a generic synapomorphy for *Hesperantha*, see Goldblatt, 1984, 2003) that extend between the filaments. Open flowers are typically held erect to suberect with the tepals spreading horizontally with the stamens symmetrically disposed. Anthers are developmentally extrorse with loculicidal dehiscence, and the pollen adheres to the dehisced anther locules. The filaments twist slightly in the open flower so that the anthers come to face inward or upward, depending on whether they are held erect (most species with colored tepals), or are articulated on the filaments, each one lying horizontally, at right-angles to the filament (crepuscular or nocturnal species with white or cream tepals). Stamens and style branches are asymmetrically disposed and declinate in *H. grandiflora*, the only species in the genus with a zygomorphic flower.

Compatibility varies within the genus. Several species have been reported to be self-compatible (Goldblatt, 1984) following hand-mediated self-pollinations but with reduced fertility (*Hesperantha bachmannii, H. cucullata, H. falcata*). Mechanical autogamy without apparent reduction in fertility occurred in *H. acuta, H. erecta, H. latifolia*, and *H. pallescens* in the absence of pollinators. *Hesperantha pauciflora* and *H. radiata* failed to set seed following self-pollinations by hand. In the course of the present study, self-compatibility was established for *H. quadrangula* and confirmed for *H. pallescens* (Goldblatt, 1984).

NECTAR

Nectar glands, when present (Table 4), are septal, as they are in the entire subfamily Crocoideae (Goldblatt, 1990, 1991; Goldblatt & Manning, unpublished). Nectar is secreted from three minute pores at the top of the ovary (one per chamber) directly into the base of the perianth tube where the accumulated fluid is retained until removed by a foraging insect. In species with the lower part of the tube narrow and tightly enveloping the style, a small amount of nectar may be present in the upper part of the tube, presumably the result of capillary action. Measurable volumes of nectar are produced in most species (Table 4), and volume correlates with tube length. The long-tubed flowers of *Hesperantha coccinea* (tube 25–38 mm long) and *H. grandiflora* (tube 28–32 mm long) produced the most nectar (up to 4.1 µl in the latter in flowers undisturbed by insects—the perianth had not fully expanded when nectar was measured), while flowers of short-tubed *H. baurii, H. falcata, H. fibrosa, H. pilosa, H. quadrangula*, and *H. radiata* produced small amounts of measurable fluid (< 1.0 µl of nectar). The smallest quantities of nectar are produced by *H. leucantha* and *H. baurii* (less than 0.1 µl in the last species). There is a negative correlation between the percentage of sugar solute in *Hesperantha* nectar and nectar volume. Thus, species that secrete the greatest amount of fluid tend to produce nectars lowest in dissolved sugars (e.g., *H. brevicaulis, H. coccinea, H. grandiflora*, and *H. woodii*), while *H. falcata, H. pilosa, H. radiata*, and *H. spicata* secrete less than 0.5 µl of fluid that contains 35% to 48% dissolved sugars. Among species that secrete less than 0.5 µl, *H. bachmannii* appears exceptional in having relatively dilute nectar, with a mean of 21.5% dissolved sugars.

Sugar analyses of *Hesperantha* flowers (Table 4) indicate that species examined for sugar composition offer nectars that are sucrose rich. White-flowered species with flowers open in the late afternoon and evening, e.g., *H. falcata, H. pilosa, H. radiata*, and *H. spicata*, have nectar of unusually high sugar concentrations, 40–50%, while *H. baurii* has nectar of 48% to > 50% sucrose equivalents. All the species with white flowers so far examined secrete nectar, although there are only trace amounts in *H. quadrangula*, but nectar presence or absence varies in species with flowers of other colors. The long-tubed flowers of *H. pubinervia* and *H. scopulosa* produce no nectar at all.

FLORAL PRESENTATION AND POLLINATION SYSTEMS

Four overlapping pollination systems can be recognized in *Hesperantha*. Comparative floral traits of the four main systems are summarized in Table 2. The pollination systems and associated floral traits do not necessarily reflect the natural relationships of species.

The Hesperantha falcata *Group*

In this group, of which *Hesperantha falcata* and *H. cucullata* are typical examples, the flowers are crepuscular or nocturnal and mostly white to cream or exceptionally pale yellow, and the perianth is salver-shaped with horizontally extended tepals (Figs. 1A, 2A) or in three species, nodding (Figs. 1D, 2B) with lightly reflexed tepals (*H. bachmannii, H. marlothii*, and *H. radiata*). The floral tube is cylindrical, expanding slightly near the apex, and hollow with a narrow, uniform diameter of about 1 mm. The tube typically contains nectar in the lower 1–3 mm. The perianth tube is usually slightly

Table 4. Nectar properties of *Hesperantha* species that produce measurable quantities of nectar (see Table 2). SD = standard deviation, (n) = number of individuals sampled, Fru = fructose, Glu = glucose, n/a = not assessed. Nectar sugars were analyzed by B.-E. van Wyk (Rand Afrikaans University, Johannesburg, South Africa). Data marked with an asterisk are from Johnson and Bond (1994). For *H. acuta* and one population of *H. falcata*, nectar from three flowers was pooled to obtain sufficient nectar to register a refractometer reading.

Hesperantha species	Nectar (n)		% Nectar sugars			Mean Sucrose/ Glu + Fru (n)
	Volume µl	Mean % sucrose equivalents (±SD)	Fructose	Glucose	Sucrose	
H. acuta	0.4–0.8 (3)	36 (pooled sample)	n/a	n/a	n/a	n/a
H. bachmannii	0.2–0.4 (8)	21.5 (2.6)	n/a	n/a	n/a	n/a
H. baurii	trace to 0.1 (6)	49–>50	n/a	n/a	n/a	n/a
H. brevicaulis	1.0–1.6 (3)	19.3 (1.5)	n/a	n/a	n/a	n/a
H. coccinea						
site 1	2.4–3.7 (5)	20.8 (1.6)	n/a	n/a	n/a	n/a
site 2	2.2–2.9 (10)	15.4 (0.9)	n/a	n/a	n/a	n/a
site 3*	1.9 (19)	17.4 (n = 11)	42	43	15	0.18 (1)
H. cucullata	0.2–0.6 (8)	40.6 (3.7)	n/a	n/a	n/a	n/a
H. falcata						
site 1	0.3–0.5 (3)	32 (pooled sample)	39	38	23	0.27 (1)
site 2	0.2–0.5 (6)	36.2 (3.5)	n/a	n/a	n/a	n/a
H. fibrosa	0.3–0.4 (4)	21.3 (2.1)	24–25	15–28	47–61	1.17 (2)
H. grandiflora	2.8–4.1 (5)	14.8 (1.0)	n/a	n/a	n/a	n/a
H. huttonii	1.3–2.4 (8)	13.7 (1.6)	n/a	n/a	n/a	n/a
H. lactea	0.1–0.6 (10)	21.6 (3.6)	n/a	n/a	n/a	n/a
H. latifolia	0.7–1.1 (10)	28.5 (3.4)	23–29	24–30	41–53	0.94 (3)
H. leucantha	0.4–1.0 (4)	46.8 (1.0)	n/a	n/a	n/a	n/a
H. marlothii	1.4–2.2 (10)	35.9 (3.8)	n/a	n/a	n/a	n/a
H. oligantha	1.1–1.8 (5)	26.4 (3.9)	19–23	24–25	52–57	1.20 (2)
H. pallescens	0.8–1.2 (10)	35.5 (5.6)	n/a	n/a	n/a	n/a
H. pauciflora	0.1–0.5 (5)	35.4 (1.7)	n/a	n/a	n/a	n/a
(pink flowers)						
(yellow flowers)	0.6–0.7 (10)	23.5 (2.4)	n/a	n/a	n/a	n/a
H. pilosa (blue flowers)	0.2–0.4 (5)	44.2 (1.9)	n/a	n/a	n/a	n/a
(white flowers)	0.1–0.5 (10)	35.7 (3.5)	n/a	n/a	n/a	n/a
site 2	0.2–0.4 (3)	45.0 (6.1)	n/a	n/a	n/a	n/a
site 3	0.2–0.5 (6)	44.8 (2.7)	n/a	n/a	n/a	n/a
H. pseudopilosa	0.2–0.5 (2)	42.0–48.5	n/a	n/a	n/a	n/a
H. radiata						
site 1	0.2–0.4 (2)	n/a	11–20	16–20	60–73	1.86 (3)
site 2	0.2–0.5 (3)	42.4 (3.9)	n/a	n/a	n/a	n/a
H. rivulicola	0.2–0.5 (3)	48.0 (2.0)	n/a	n/a	n/a	n/a
H. spicata	0.2–0.5 (2)	42–45	n/a	n/a	n/a	n/a
H. stenosiphon	4.2–6.5 (11)	17.5 (2.0)	n/a	n/a	n/a	n/a
H. sufflava	0.4–1.2 (10)	28.0 (2.6)	n/a	n/a	n/a	n/a
H. woodii	1.2–1.8 (5)	18.1 (0.9)	n/a	n/a	n/a	n/a

shorter than the tepals, thus 7–16 mm long (Table 2) compared to tepals 12–16 mm long, but the tube is half again as long as the tepals in *H. flava*, 20–26 mm long, compared with tepals up to 16 mm long.

Almost all white- to pale yellow-flowered species of the southern African winter-rainfall zone are crepuscular or fully nocturnal (Table 3). The perianth opens in the late afternoon, typically after 16:00 H or at sunset, and closes before sunrise. *Hesperantha pauciflora* is an exception. A rare, pale yellow-flowered form of this otherwise pink-flowered species (Goldblatt, 2003) has the tepals opening soon after midday and closing before sunset. *Hesperantha quadrangula* is unusual: its white flowers have an unusually short perianth tube, 2–3 mm, compared to the tepals, 9–12 mm long, and they open at ca. 16:00 H and close shortly after sunset but before dark, ca. 19:00 H. The widespread and common *H. falcata* is notable for the varied times that flowers

Figure 1. Growth forms and plant habit in *Hesperantha*. —A. *H. acuta*. —B. *H. humilis*. —C. *H. oligantha*. —D. *H. radiata*. Scale bar = 10 mm for A, B, and D; 15 mm for C. (Drawn by Margo Branch, Cape Town.)

of different populations open, some opening as early as 16:00 H, and others after 17:30 H, but in all populations we examined, the flowers remain open after 21:00 H. In *H. erecta*, the perianth opens at ca. 15:00 H.

The eastern southern African *Hesperantha lactea*, *H. hygrophila* Hilliard & Burtt, *H. inconspicua* (Schltr.) G. J. Lewis, and *H. rupestris* N. E. Br. ex R. C. Foster (the latter three not studied here) have unscented, diurnal flowers with a white to cream perianth that are open for only a portion of the day and close fully before sunset, between midday and

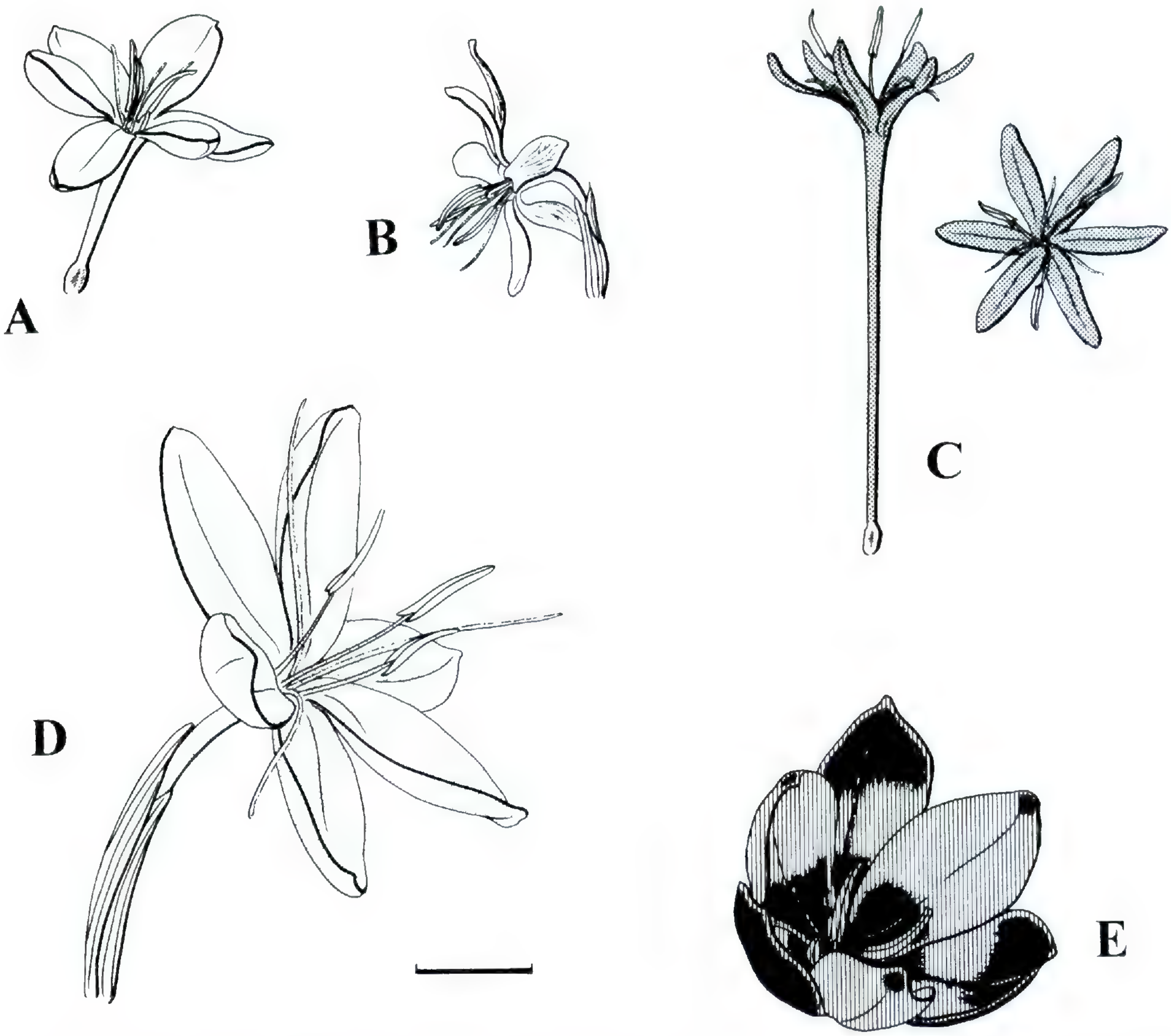

Figure. 2. Perianth types in *Hesperantha*. —A. *H. sufflava*. —B. *H. radiata*. —C. *H. oligantha*. —D. *H. coccinea*. —E. *H. raginata*. Scale bar = 10 mm. Shading code: dark stippling = purple (*H. oligantha*); light stippling = red (*H. coccinea*); vertical hatching = yellow; and solid black = brown (*H. raginata*). Drawn by John Manning.

late afternoon depending on the species (Hilliard & Burtt, 1986; Goldblatt, 2003). Thus in all respects except perianth color they resemble more closely species of the next group, the *H. pauciflora* group.

When open, the flowers of species belonging to the *Hesperantha falcata* group produce a strong, sweet fragrance that is variable between, and sometimes within, species. Scents range from light rose (*H. quadrangula, H. rivulicola*) to jasmine or frangipani (*Plumeria*) (*H. cucullata, H. falcata*—some populations; *H. flexuosa, H. pilosa*—some populations), narcissus (*H. spicata*), acrid-musk (*H. erecta, H. falcata*—some populations; *H. pilosa*—some populations; *H. sufflava*), or sweet with a strong clove component (*H. marlothii, H. radiata*).

Hesperantha cucullata, H. pilosa, H. quadrangula, H. rivulicola, H. sufflava, and sometimes *H. falcata* are actively visited by large-bodied apid bees (Tables 5, 6) with probosces 3–10 mm long. Bees forage for both pollen and nectar soon after the flowers open in the late afternoon. The white flowers are conspicuous in the late afternoon light, and *Anthophora* species or *Apis mellifera* can often be seen visiting the flowers of these species. Small settling nocturnal moths, mostly noctuids, and most commonly *Heliotis armigera*, but also species of Adelidae, Drepanogynidae, Geometridae, and Pyralidae (Tables 5, 6), with probosces 4–12 mm long are common and active at or after sunset and in the early evening in the southern African winter-rainfall zone, and regularly visit flowers of all the species we observed for pollinators after sunset (*H. bachmannii, H. cucullata, H. falcata, H. marlothii, H. pilosa, H. pseudospicata, H. radiata*, and *H. rivulicola*). Both bees and moths are polylectic foragers, and individual bees were found to carry the pollen of co-blooming species (Table 6), including

Table 5. Length of mouth parts of insects captured on *Hesperantha* flowers, with perianth tube lengths. Measurements are ranges for the insect or plant populations studied.

Insect species	Mouth part mm (n)	Plants on which insect captured	Tube length mm
Diptera			
Prosoeca ganglbauri	27–30 (4)	*H. grandiflora, H. scopulosa*	28–42
P. ganglbauri	28–32 (4)	*H. woodii*	35–38
P. peringueyi	20–25 (3)	*H. latifolia*	15–25
P. sp. nov. 2	ca. 9 (2)	*H. pauciflora*	6–8
Stenobasipteron wiedemannii	19–23 (3)	*H. huttonii*	25–35
Hymenoptera			
Amegilla capensis	9–10 (3)	*H. baurii*	8–10
Anthophora diversipes	6.5–8 (4)	*H. cucullata, H. pauciflora, H. pilosa, H. rivulicola,*	6–12
		H. sufflava	12–16
Apis mellifera	3–4 (10)	*H. baurii, H. cucullata, H. falcata*	7–10
Lepidoptera [butterflies]			
Aeropetes	ca. 30 (1)	*H. coccinea*	30–38
Papilio demodocus	ca. 25 (1)	*H. coccinea*	30–38
P. nireus	22 (1)	*H. coccinea*	30–38
Lepidoptera [moths]			
Agrotis segetum	ca. 11 (1)	*H. rivulicola*	8–11
Ceromitia sp.	11–12 (7)	*H. pseudopilosa, H. radiata, H. rivulicola*	8–12
Cucullia terensis	ca. 12 (3)	*H. cucullata, H. pilosa*	7–10
Drepanogynis sp.	ca. 10 (1)	*H. rivulicola*	8–11
D. dochmoleuca	ca. 7 (1)	*H. pilosa*	9–10
D. rufigrisea	ca. 11 (1)	*H. bachmannii*	8–10
Heliotis armigera	8–9 (6)	*H. bachmannii, H. cucullata, H. pseudopilosa, H. radiata*	8–12
Nomophila noctuella	5–7 (6)	*H. cucullata, H. pseudopilosa, H. radiata*	7–12
Perizoma artifex	ca. 4 (1)	*H. pilosa*	9–10
Xylopteryx arcuata	ca. 8 (2)	*H. cucullata*	7–9

Bulbinella (Asphodelaceae), *Lachenalia* (Hyacinthaceae), *Hermannia* (Malvaceae), and Iridaceae (including *Gladiolus, Moraea*) in their scopae or corbiculae and/or on various parts of their bodies. In contrast, only *Hesperantha* pollen was found on the bodies of captured moths except for one visiting *H. pilosa*, but as there were no other obvious night-flowering species at most of our study sites this is not surprising.

All moths captured while visiting *Hesperantha* flowers settled on the inflorescence and crawled over the flowers. They carried pollen on the underside of the wings, ventral part of the thorax, legs, and sometimes on the antennae and proboscis. One moth captured on *Cyphia bulbosa* (L.) P. J. Bergius (Campanulaceae) at our *H. pilosa* study site carried pollen of that species as well as that of *H. pilosa*. Pollen loads were light, often only a few grains being present. The bodies of moths are, however, poor surfaces for carrying pollen, and it is not surprising that after capture in a net and transfer to a killing bottle very little pollen remained on their bodies by the time they had been pinned and then examined. Moth activity was found to be at a maximum for the first hour and a half after sunset, thus until about 20:30 H. After this we noted few, if any, moth visits and we therefore did not continue our observations. It is possible that other moth species become active later, as noted by Johnson et al. (1993) for *Crassula fascicularis* Lam. (Crassulaceae), but flowers of most crepuscular or nocturnal *Hesperantha* species close before 1:00 H, exceptions being *H. marlothii, H. radiata,* and *H. rivulicola*, the flowers of which remain open until dawn or daylight.

The pollination by small settling moths in *Hesperantha* follows the pattern described by Johnson (1997) for species of the orchid genus *Satyrium*.

Johnson recorded a similar suite of moths visiting different species of that genus at night: *Heliotis armigera* and *Syngrapha circumflexa* on *S. bicorne* (L.) Thunb. and *Agrotis segetum* on *Satyrium ligulatum* Lindl. and *S. stenopetalum* Lindl. with the butterfly *Vanessa cardui* also visiting *S. ligulatum* during the day, a pattern paralleled in *H. rivulicola*. A high nectar sugar concentration of 40.1% was also noted for *S. stenopetalum*, which is comparable to the high nectar sugar concentrations we found in most settling moth-pollinated species of *Hesperantha*.

Those white-flowered species with flowers opening at or after sunset, including *Hesperantha flava*, *H. marlothii*, and *H. radiata*, have not been seen to be visited by bees. The long-tubed *H. flava* may receive visits from sphinx moths according to Vogel (1954), but while this is consistent with its long perianth tube (18–28 mm long), we assume that Vogel was only making a suggestion and did not observe sphinx moths visiting the species. Among the white-flowered species of the winter-rainfall zone *H. quadrangula* is exceptional in having flowers that close at about sunset, that is, before moths are normally active. Thus, although it has white flowers that open in the late afternoon, it is evidently not pollinated by moths.

The Hesperantha pauciflora *Group*

The *Hesperantha pauciflora* group (Table 2) includes the common eastern southern African *H. baurii*, its allies, *H. lactea*, *H. leucantha*, *H. similis*, and several more, the western Cape *H. pauciflora*, and western Karoo *H. humilis* (Fig. 1B). The perianth coloration is usually pink to purple, but blue or mauve in some populations of *H. pilosa* and in *H. ciliolata*, and cream to pale yellow in *H. lactea*. Floral structure in this group is virtually identical to that of the *H. falcata* group, but the flowers are typically scentless (Table 2) and the tepals unfold during the day, often in the morning, and close at midday or shortly thereafter (*H. baurii*, *H. pilosa*—blue form, *H. similis*), or in the early afternoon, then closing by 17.30 H (*H. pauciflora*). *Hesperantha ciliolata* is exceptional in having fragrant flowers that produce an unusual acrid, musky scent reminiscent of that produced by some southern African species of the orchid genera *Corycium* and *Pterygodium*, and differing markedly from the sweet odors of species of the *H. falcata* group. Flowers of the *H. pauciflora* group produce small quantities of nectar, mostly 0.1–0.3 μl in volume (Table 4). Flowers actively visited by bees may, however, contain no detectable nectar when sampled in the field. When sampled later, after placing cut stems in water overnight, flowers yield nectar, indicating that visiting insects may have removed all available nectar during their foraging, or alternatively insufficient water was available to plants to allow nectar production.

Species in this group are pollinated primarily by large-bodied female anthophorine bees or worker honey bees foraging for pollen or nectar, or for both rewards. Bees land on the flower and brush both the anthers and stigma lobes as they crawl over the perianth while scraping pollen into their scopae or corbiculae. Most apid bees, *Amegilla*, *Anthophora*, and most *Apis mellifera* workers captured on *Hesperantha* flowers are polylectic foragers (Table 6), and individuals were found to carry the pollen of co-blooming Fabaceae, Asphodelaceae, Hyacinthaceae, Boraginaceae, and Iridaceae in their scopae or corbiculae and on various parts of their bodies. Perhaps significantly, however, almost half the *Apis mellifera* workers captured, 11 out of 26 individuals, carried pure loads of *Hesperantha* pollen, indicating temporary floral constancy, unlike other bees analyzed for their pollen loads (Table 6). Flowers of *H. pauciflora* are occasionally also visited by a relatively short-proboscid *Prosoeca* species, presently undescribed (Table 6), which behave much as anthophorine bees in search of nectar.

Species of this group may also be visited by hopliine beetles, but the significance of these beetles compared to bees visiting the same species is difficult to assess. Hopliine beetles often visit a range of plant species with the large, brightly colored flowers that are particularly suited to their activities (Picker & Midgely, 1996; Goldblatt et al., 1998b), which include assembly, competitive behavior, and copulation. Nevertheless, it may be best to regard species visited by both bees and hopliine beetles as exploiting both groups of pollinators.

The Hesperantha latifolia *Group (Table 2)*

The Namaqualand and western Karoo species, *Hesperantha latifolia* and *H. oligantha*, and the eastern southern African *H. brevicaulis*, *H. grandiflora*, *H. huttonii*, *H. scopulosa*, *H. stenosiphon*, and *H. woodii* exemplify the third pollination category (Figs. 1C, 2C). In these species the flowers are odorless, have an elongate perianth tube 20–60 mm long, and usually a pink to purple (rarely red) perianth. The tepals are shorter than the tube, mostly 15–25 mm long (exceptionally to 42 mm in *H. scopulosa* and to 38 mm in *H. grandiflora*), and spread horizontally, or are slightly cupped in *H. stenosiphon* and *H. woodii*. Exceptional in the group and genus, *H. grandiflora* has the tube sharply bent

Table 6. Pollen load analysis of captured insects on *Hesperantha* species. Coleoptera: Scarabaeidae: *Anisochelus*, *Anisonyx*, *Clania*. Hymenoptera: Apidae: *Allodape*, *Amegilla*, *Anthophora*, *Apis*. Colletidae: *Scrapter*. Halictidae: *Patellapis*. Melittidae: *Rediviva*. Diptera: Nemestrinidae: *Prosoeca*, *Stenobasipteron*. Lepidoptera: Adelidae: *Ceromitia*. Drepanogynidae: *Drepanogynis*. Geometridae: *Perizoma*, *Xylopteryx*. Noctuidae: *Agrotis*, *Cucullia*, *Heliotis*. Nymphalidae: *Vanessa*. Pieridae: *Papilio*. Pyralidae: *Nomophila*. Satyridae: *Aeropetes*. Sphingidae: *Hippotion*. Data for *Hesperantha vaginata* are from Goldblatt et al. (1998b) and those for *H. latifolia* are from Manning and Goldblatt (1996). Site numbers refer to study sites as indicated in Table 1.

Plant and insect taxon	Number of insects carrying pollen load(s): Pollen from host flower alone	Pollen from host flower plus other species
H. baurii		
site 1		
Amegilla capensis ♀	0	3
Patellapis sp. ♀	0	1
Rediviva nelii ♀	0	6
hopliine beetle 1	0	1
hopliine beetle 2[1]	3	3
site 2		
Apis mellifera	5	0
H. bachmannii		
Drepanogynis rufigrisea	1	0
Heliotis armigera	1	0
unidentified noctuid moth	1	0
H. brevicaulis		
Stenobasipteron wiedemannii	not captured	
H. coccinea		
site 2		
Papilio nireus	1	0
Papilio demodocus	1	0
site 3		
Aeropetes tulbaghia	1	0
H. cucullata		
Anthophora praecox ♀	0	1
A. schulzei 1 ♀ 1 ♂	0	2
Apis mellifera	3	0
Cucullia terensis	1	0
Heliotis armigera	4	0
Nomophila noctuella	3	0
Xylopteryx arcuata	2	0
H. erecta		
Apis mellifera	0	5
Anthophora rufidicaudis ♀	0	2
H. falcata		
site 1		
Apis mellifera	1	4
site 2		
(moths incl. *Heliotis armigera* seen but not captured)		
H. flexuosa		
Anthophora praecox ♀	0	2
Apis mellifera	0	2
H. grandiflora		
Prosoeca ganglbauri	0	3
H. huttonii		
Stenobasipteron wiedemannii[1]	0	3
H. lactea		
Allodape stellarum ♀	0	2
H. latifolia		
Prosoeca peringueyi	0	4

Table 6. Continued.

Plant and insect taxon	Number of insects carrying pollen load(s)	
	Pollen from host flower alone	Pollen from host flower plus other species
H. luticola		
Apis mellifera	0	2
H. marlothii		
Cuculia terensis	1	0
(*Hippotion celerio* seen but not captured)		
H. pauciflora (pink flowers)		
site 1		
Apis mellifera	0	4
site 2		
Anisochelus inornatus[1]	2	3
Anthophora schulzei ♀	0	2
Prosoeca sp. nov.	0	2
(yellow flowers)		
Anisochelus inornatus	2	1
Anthophora diversipes ♀	0	1
Apis mellifera	2	0
H. pilosa (blue flowers)		
Apis mellifera	2	3
Anthophora schulzei ♀	0	1
Anthophora krugeri ♀	0	1
Anthophora diversipes ♀		
(white flowers)	0	1
Anthophora rufidicaudis ♀	0	2
Cucullia terensis	2	0
Drepanogynis dochmoleuca	1	0 (1 with no pollen)
Perizoma artifex	1	0
H. pseudopilosa		
Ceromitia sp.	2	0
Drepanogynis rufogrisea	1	0 (1 with no pollen)
Heliotis armigera	4	0 (5 with no pollen)
Heliotis scutuligera	1	1
Nomophila noctuella	4	0 (2 with no pollen)
(*Hippotion celerio* was captured but did not contact style branches or anthers and carried no *Hesperantha* pollen)		
H. quadrangula		
Apis mellifera	0	2
Anthophora diversipes ♀	0	2
Scrapter sp. indet. ♀	0	1
Anisonyx ignitus	0	1
H. radiata		
Ceromitia sp.	2	0
Heliotis armigera	1	0
Nomophila noctuella	1	0
H. rivulicola		
Anthophora diversipes ♀	0	4
Agrotis segetum	1	0
Ceromitia sp.	3	0 (1 with no pollen)
Drepanogynis sp.	1	0
(*Vanessa cardui* was not captured but individuals were seen to contact anthers and style branches on visits)		
H. scopulosa		
Prosoeca ganglbauri	0	3
H. similis		
Amegilla capensis ♀	0	2
H. stenosiphon		
Apis mellifera[1]	3	2

Table 6. Continued.

Plant and insect taxon	Number of insects carrying pollen load(s)	
	Pollen from host flower alone	Pollen from host flower plus other species
H. sufflava		
Apis mellifera	0	2
Anthophora rufidicaudis ♀	0	2
Anthophora krugeri ♀	0	1
Anisonyx ditus	0	3
Scrapter sp. nov. ♀	0	2
Scrapter aff. *albitarsis* ♀	0	2
H. vaginata		
Clania glenlyonensis[2]	7	5
H. woodii		
Prosoeca ganglbauri	2	3
Total	74	105

[1] = more individuals seen but not captured.
[2] = *Lepisia* sp. of Goldblatt et al. (1998b).

near the apex so that the flowers face to the side, with the tepals held more or less vertically. The stamens and style branches of this species are unilateral with the anthers and style arms arching downward. Flowers of the *H. latifolia* group typically produce relatively large quantities of nectar (Table 4), mostly 1–4 µl in volume with concentrations ranging from 14.8 to 28.5% sucrose equivalents. Eastern southern African species have unusually low nectar concentrations, less than 21% sucrose equivalents and with a mean as low as 14.8% in *H. grandiflora* and 13.7% in *H. huttonii*. The flowers of *H. scopulosa* lack nectar, as do those of *H. pubinervia* (for which we have no pollinator observations). The long-tubed flowers of the rare *H. pubinervia* have an unusually narrow tube (Goldblatt, 2003), which may not accommodate the proboscis of a long-proboscid fly.

Flowers of most species in the *Hesperantha latifolia* group are visited and pollinated exclusively by long-proboscid flies in the family Nemestrinidae. In the southern African winter-rainfall zone, the long-tubed *H. latifolia* is pollinated by the nemestrinid *Prosoeca peringueyi*, while *H. oligantha* and *H. purpurea* are inferred to be pollinated by a second and undescribed *Prosoeca* species, *P.* sp. nov. (see Goldblatt et al., 1995; Manning & Goldblatt, 1996). Long-tubed species of the summer-rainfall zone, including *H. grandiflora*, *H. scopulosa*, and *H. woodii*, are pollinated by *P. ganglbauri*, while *H. brevicaulis* and *H. huttonii* are pollinated by *Stenobasipteron wiedemannii*. The elongated proboscs of these flies are typically slightly shorter than the length of the perianth tubes of the *Hesperantha* species that they visit (Table 5), but these flies are the only insects that are able to forage on the nectar held in the lower part of the perianth tube. While flowers of *H. stenosiphon* seem obviously adapted for long-proboscid fly pollination, we found no flies at our study site; instead, honeybees were visiting the flowers and collecting pollen. In doing so they were seen transporting pollen from anthers of one plant to style branches of another, effecting pollination.

An important exception in the *Hesperantha latifolia* group is the red-flowered form of the riverine species *H. coccinea* (Fig. 2D). This plant has two color morphs, the more common red-flowered form pollinated by a guild of large butterflies including *Aeropetes tulbaghia* (Satyridae) and *Papilio* species (Papilionidae). Visits by *Aeropetes* have also been reported by Johnson and Bond (1994). Johnson (pers. comm.) has also seen an unidentified long-proboscid fly visiting the red-flowered form, but this has been witnessed only once to date. The second color form of *H. coccinea* has a pink perianth. We have no observations on visitors to the pink form. Its pink perianth may indicate a dependence on long proboscid flies for pollination. Because only one color form of one species of *Hesperantha* is pollinated by large butterflies, it seems unreasonable to recognize an additional pollination group in the genus.

Flies grasp the tepals with their tarsi and probe for nectar while continuing to vibrate their wings, contacting anthers and stigmas with the ventral or lateral parts of the head and thorax. In the case of *Hesperantha grandiflora*, pollen deposition is always on the ventral part of the thorax because the unilateral stamens are positioned below the mouth

of the floral tube. Field observations and pollen load analyses show that all fly species visit open flowers of other species during foraging bouts and that most of these species have morphologically convergent flowers that may be regarded as belonging to specific pollination guilds. Thus, *Prosoeca peringueyi* visits a range of plants with intense red or violet flowers, including *Pelargonium magenteum* J. J. A. van der Walt (Geraniaceae) and species of Iridaceae such as *Babiana curviscapa* G. J. Lewis, *B. dregei* Baker, and *Lapeirousia silenoides* (Jacq.) Ker Gawl. (Manning & Goldblatt, 1996), as well as *H. latifolia* in the Kamiesberg of Namaqualand. Likewise, *Prosoeca ganglbauri* visits several pink-flowered species including *Gladiolus microcarpus* G. J. Lewis (Iridaceae), *Nerine bowdenii* S. Watson (Amaryllidaceae), and *Zaluzianskya microsiphon* (Kuntze) K. Schum. (Scrophulariaceae) during foraging bouts on *H. grandiflora* or *H. scopulosa* in the northern Drakensberg.

The Western Cape *Hesperantha pallescens* is exceptional in having pale yellow flowers with an elongate perianth tube with the flowers opening soon after sunrise and closing before sunset. The flowers conform to the model for species pollinated by another long-proboscid fly, *Philoliche* (Tabanidae) (Goldblatt et al., 1995; Goldblatt & Manning, 2000). To date we have not located a study population at an undisturbed site where the predicted pollinator is active, and we have seen no insect visitors to the species at our study site during apparently ideal conditions for insect activity.

Two patterns of butterfly behavior can result in pollen dispersal and pollen deposition. The first has been described as "inspection visitation" by Johnson and Bond (1994). A butterfly making an inspection visit does not land or feed on a flower, but its comparatively long body and broad wings often brush against the anthers and long style branches or stigmas as it swoops close to an open flower before moving to another, sometimes of the same species. In contrast, a true foraging visit requires that the butterfly actually grasp the tepals and insert its proboscis into the floral tube. In doing so, the ventral surface of the thorax and proximal abdomen become dusted with pollen. Butterflies noted and captured visiting red-flowered *Hesperantha coccinea* include *Papilio demodocus*, *P. nereis*, and *Aeropetes tulbaghia*, the latter also reported by Johnson and Bond (1994) to be a pollinator of this plant.

The Hesperantha vaginata *Group*

The *Hesperantha vaginata* group (Table 2) includes only *H. vaginata* and *H. karooica* Goldblatt (not studied), which have unscented, bright yellow flowers, often marked with bold splashes of contrasting dark brown color (Fig. 2E). These flowers have a relatively short tube, 5–8 mm long, that produces no measurable nectar. The tepals, 30–35 mm long, much exceed the length of the tube. These flowers open during the middle part of the day, 13:00 H in *H. vaginata*, and close in the late afternoon, ca. 18:00 H in warm weather.

Hesperantha vaginata is visited exclusively by the hopliine beetle *Clania glenlyonensis* (identified as *Lepisia* sp. 1 in Goldblatt et al., 1998b) (Table 6). The flowers have the stereotyped adaptations for the hopliine beetle pollination system, a large flower with spreading or somewhat cupped tepals, reduced perianth tube, absence of nectar, and bold contrasting pigmentation (so-called beetle marks) (Picker & Midgley, 1996; Goldblatt et al., 1998b; Steiner, 1998). *Clania* individuals spend a considerable time in a flower, either crawling about or at rest with their heads pointed toward the center for up to 20 minutes. Sometimes their visits may last much longer, and beetles may even spend the night in the closed flowers. Hopliine beetles use the flowers of *H. vaginata* and some other species growing nearby, including *Romulea monadelpha* (Sweet) Baker (Iridaceae) and *Arctotis acaulis* L. (Asteraceae), as sites for assembly, intraspecific competition, and mating. They are invariably covered with a combination of pollen of *H. vaginata* and the co-blooming species listed above. Although these beetles feed on pollen and sometimes on tepal tissue, they do little or no damage to flowers (Steiner, 1998; Goldblatt et al., 1998b).

Discussion

Pollination biology varies among *Hesperantha* species but correlates closely with the mode of floral presentation, timing of anthesis, and nectar secretion. Contrary to past predictions (Scott Elliot, 1891; Marloth, 1915; Vogel, 1954), white-flowered species that have flowers opening in the late afternoon and remaining open at night are not exclusively pollinated by moths. Indeed, our studies of the floral biology of *Hesperantha*, incomplete as they are, highlight the danger of inferring the pollination systems of plants with limited fieldwork or entirely from floral morphology. Marloth (1915: plate 42) suggested the genus was primarily pollinated by moths, based on his observation of small moths (not identified) seen visiting *H. falcata*. Vogel (1954) carried this further in suggesting that long-tubed species including *H. flava*, *H. grandiflora*, *H. longituba* (by which he probably meant *H. huttonii*),

and *H. pulchra* were pollinated by sphinx moths. The last three species have odorless, pink flowers that close at night. Vogel also speculated that the yellow and brown, short-tubed flowers of *H. vaginata* (which he knew as *H. metelerkampiae*) and the pink-flowered *H. pauciflora* were pollinated by bees (Vogel, 1954: 103). He was partly correct only in his assessment of *H. pauciflora*, and possibly of *H. flava*, for which we await field observations.

At first glance the adaptive radiation of pollination systems in *Hesperantha* parallels that found in larger genera of the Iridaceae in southern Africa, but with an unusual emphasis on white flowers opening in the late afternoon or evening, a pattern best developed in the southern African winter-rainfall zone. Specifically, Bernhardt and Goldblatt (2000) noted the number of pollination systems in an African genus of the Iridaceae correlates positively with the number of species in the genus. Genera containing more than 100 species (e.g., *Gladiolus* and *Moraea*) have the most diverse pollination systems exploiting up to eight broad categories of pollen vectors. With the exception of *Ferraria* (ca. 12 species) and *Sparaxis* (15 species), genera of Iridaceae with less than 20 species (e.g., *Micranthus*, *Nivenia*) do not have more than two modes of animal pollination (Goldblatt et al., 2000a; Bernhardt & Goldblatt, 2000; unpublished data). *Hesperantha*, with 79 species, *Geissorhiza* (85 spp.), *Ixia* (ca. 50 spp.), and *Lapeirousia* (40 spp.) each have four or five major pollination modes (Goldblatt et al., 1995, 2000b; Bernhardt & Goldblatt, 2000).

Four major modes of pollination (bee and crepuscular settling moth; diurnal bee; hopliine beetle; long-proboscid fly, or large butterfly) are confirmed for *Hesperantha* based on our field observations and collection of floral foragers with analysis of their pollen loads. A fifth mode of pollination by sphingid moths, predicted by Vogel (1954) for *H. flava*, remains to be confirmed by future field investigation.

Furthermore, pollination systems in *Hesperantha* also subdivide along predictable modes of floral presentation already described in other genera of Iridaceae. This is most striking in the *H. latifolia* group where tubular, odorless flowers with different patterns of floral pigmentation are pollinated by different genera or species of two families of long-proboscid flies. As described in the genera *Babiana*, *Gladiolus*, and *Lapeirousia*, tubular flowers that are pink to the human eye (e.g., *H. brevicaulis*, *H. grandiflora*, *H. huttonii*, *H. woodii*) are most likely to be pollinated by the Nemestrinidae *Prosoeca ganglbauri* and *Stenobasipteron wiedemannii*. In contrast, those with intense blue to purple flowers (e.g., *H. latifolia*, *H. oligantha*) are pollinated by *Prosoeca peringueyi* or an undescribed *Prosocea* species. Pale yellow to cream, tubular flowers are more likely to be pollinated by long-proboscid tabanids in the genus *Philoliche* (Goldblatt et al., 1995; Goldblatt & Manning, 2000; Manning & Goldblatt, 1996, 1997).

UNIQUE TRENDS IN THE FLORAL ECOLOGY OF *HESPERANTHA*

Pollination systems incorporating large-bodied bees, long-proboscid flies, or hopliine scarab beetles have been well described in 14 other genera of the Iridaceae of southern Africa and are not in any manner unusual in *Hesperantha* (Bernhardt & Goldblatt, 2000). There are, however, two modes of pollination in this genus atypical of the family. First, pollination by deceit is suggested in the tubular, pink flowers of *H. pubinervia* and *H. scopulosa*. While both species have the pigmentation and floral tube length of nectariferous species pollinated by long-proboscid flies, both fail to secrete nectar. As this mode of floral presentation is virtually identical in co-blooming species pollinated by the same flies, *H. pubinervia* and *H. scopulosa* evidently represent either Batesian or guild mimics. These two modes of deceit are more common in the Orchidaceae (Dafni & Bernhardt, 1989), including the southern African genus *Disa* (Johnson, 1994; Johnson et al., 1998). Second, our documentation of pollination mechanisms in the *Hesperantha falcata* group is the first record in the Iridaceae of species either exploiting both settling moths of five lepidopteran families with crepuscular to nocturnal foraging habits and large-bodied apid bees (*Anthophora* and *Apis*), or settling moths alone. While generalist pollination systems combining bees and Lepidoptera have been described in a few species of *Lapeirousia* (Goldblatt et al., 1995), these species depend on true butterflies and sometimes moths with diurnal habits. In contrast, full floral presentation by species of the *H. falcata* group begins at twilight. Thus, while several species of the *H. falcata* group attract large-bodied bees, *Gladiolus* and *Lapeirousia* species receive the majority of their visits from bee pollinators from mid morning to early afternoon, and their flowers often close at night. Bee pollination in the *H. falcata* group only begins at the end of the day, and flowers remain open after sunset to exploit a second group of pollinators that belong to another order of insects.

Other genera of the African Iridaceae in which moth pollination is known or inferred, *Babiana* (un-

published data), *Gladiolus* (Goldblatt et al., 2001; Goldblatt & Manning, 2002), and *Lapeirousia* (Goldblatt et al., 1995), have larger flowers with a relatively long perianth tube, and are visited either by hovering sphinx or noctuid moths with long probosces. The foraging pattern in these species is unlike that shown by small moths on *Hesperantha* flowers, in which individuals crawl over the inflorescence, visiting one flower after another before moving to another plant.

The dark red or brown pigmentation on the reverse of the outer tepals of most otherwise white-flowered species of the *Hesperantha falcata* group may be a form of crypsis. When the perianth is closed, only the outside of the outer tepals is visible, and the dark color presumably camouflages the perianth from both herbivorous beetles and nectar-robbing bees. Johnson (1995) postulated a similar reason for the dark red color of the orchid *Disa* (*Monadenia*) *ophyridea* (Lindl.) Bolus, which is also pollinated by noctuid moths. These flowers cannot close fully, hence the heightened need for cryptic coloration to prevent nectar and pollen robbers. In this species moths evidently locate flowers solely by olfactory cues.

At first glance, butterfly pollination in *Hesperantha coccinea* appears to converge with the *Aeropetes tulbaghia* pollination system described by Johnson and Bond (1994). These authors have described a true guild of red-flowered species that bloom primarily in the southern African winter-rainfall zone and are pollinated almost exclusively by the large satyrid butterfly *A. tulbaghia*. This guild includes several species in the Amaryllidaceae and Iridaceae and is characterized by the large, bright red flowers, sometimes with white nectar guides, relatively narrow floral tubes and ample, but relatively dilute nectar. Although it occurs in the southern African summer-rainfall zone, *Hesperantha coccinea* appears to fit this profile, but more important, it is not pollinated exclusively by *Aeropetes*, unlike the guild of large butterfly flowers in the winter-rainfall zone. The pollination system of *H. coccinea* also incorporates some of the larger species of butterflies in the family Papilionidae. Thus even though *Aeropetes* has a strong, innate attraction for red flowers, it is not the only visitor to red butterfly flowers in southern Africa. The lack of pollination by other large butterflies in the winter-rainfall zone may simply reflect the seasonal scarcity of other large butterflies there. We note that other large butterfly flowers of the summer-rainfall zone include red-flowered species such as *Bauhinia galpinii* N. E. Br. (Fabaceae), *Gloriosa superba* L. (Colchicaceae), as well as those of other colors such as blue-flowered *Plumbago auriculata* Lam. (Plumbaginaceae). In eastern southern Africa *Aeropetes* seems to have a weaker affinity for red flowers and often visits yellow flowers of *Kniphofia* (Asphodelaceae), in addition to the red flowers of plants such as *Gladiolus saundersii* J. D. Hook. (Goldblatt & Manning, 2000, 2002) as well as *H. coccinea*. It is unlikely that red pigmentation and tubular flowers limit the access of large butterflies other than *A. tulbaghia* in the classic definition of butterfly pollination (Faegri & van der Pijl, 1979), in which red pigmentation and a narrow floral tube are relatively common.

POLLINATION SHIFTS IN *HESPERANTHA*

With the exception of species of the *Hesperantha falcata* group, pollination systems in this genus reflect the exploitation of the usual range of southern African insects responsible for pollination in the family. In contrast to other genera of Iridaceae, however, we also note that minimal shifts in floral characters are all that has been required to change a pollination system.

In particular, the morphological modification of *Hesperantha* flowers has been limited to the length of the perianth tube and the orientation of the tepals at anthesis. This conservative trend must be compared to the shifts in the pollinations systems of *Moraea* requiring severe changes in tepal orientation and differentiation of the inner and outer tepals and in the morphology of the staminal column and style branches (Goldblatt & Bernhardt, 1999). We must also compare the relatively conservative perianth morphology of *Hesperantha* with that of *Gladiolus* in which floral symmetry and floral tube shape and orientation change with the primary pollinators (Goldblatt & Manning, 1998; Goldblatt et al., 1998a). Instead, significant alterations of floral presentation in *Hesperantha* are limited to relatively minor shifts in floral pigmentation, correlated with variation in scent production and nectar secretion. Indeed, to the human eye *Hesperantha* flowers appear to lack the unusually complex, contrasting patterning of pigmentation typical of the flowers of most other genera of the family in southern Africa.

Comparatively minor differences in nectar sugar composition and concentration have had a dramatic effect on which insects are most likely to pollinate a *Hesperantha* flower, for the important reason that these biochemical characters evolved in association with shifts in the mechanics of floral phenology. Specifically, the stereotyped opening and closing of tepals in different species, at different seasons, and

at different times of the same day sharply restricts foraging by prospective pollinators. Mature flowers that remain closed while particular species of anthophilous insects are actively searching for edible rewards are almost as effectively excluded from developing novel interactions as they would be if they bloomed at a time of the year when the same insects are absent.

A change in pollinator from an insect with relatively short mouth parts, such as apid bees, short-proboscid nemestrinids, small moths, and possibly other polyphagic taxa, to one with longer mouth parts, such as long-proboscid nemestrinids, may seem a relatively moderate shift and merely one of degree. It must, however, be remembered that a shift to a long-proboscid fly pollinator means a change from a system where several species of bee and fly, or several different species of moth, may pollinate a species to one where only a single species is the primary or sole pollinator. Long-proboscid flies are particularly effective pollinators of certain plants because relatively few plants offer them a reliable source of nectar, and they usually carry heavy loads of pollen on specific parts of their bodies, limiting or avoiding stigma clogging (Goldblatt & Manning, 2000). The shorter-tongued insects, however, visit many species, sometimes in a nonconstant pattern, and they usually carry mixed loads of pollen that are often randomly scattered over their bodies. These contrasting patterns of pollination must have important consequences for the reproductive systems of the two plant groups. A shift to a specialist pollination system using just one pollinator species presumably has important consequences for the radiation of a genus despite the apparently trivial shift in morphology and physiology.

DISTRIBUTION OF POLLINATION SYSTEMS

In the absence of any phylogenetic hypotheses about the radiation of *Hesperantha*, the origin and evolution of pollination systems in the genus remains a speculative topic. Small white, crepuscular or nocturnal flowers are unknown in subfamily Crocoideae outside the genus, and this pollination system must be derived. Flowers in *Geissorhiza*, the genus to which *Hesperantha* is most closely related (Lewis, 1954; Goldblatt, 1984; Reeves et al., 2001), may be pink, blue, violet, or white, but are always diurnal. The most common, and presumably ancestral pollination system in *Geissorhiza* is a generalized one (Nänni, unpublished data) in which the small, short-tubed flowers are open during the day and offer both pollen and small quantities of nectar. They are visited by a range of insects including *Apis mellifera*, hopliine beetles, butterflies, bee flies (Bombyliidae), and short-proboscid tabanid and nemestrinid flies, and these species may be considered generalists. The pollination system in *Hesperantha* that most closely resembles this system is the large-bodied *Apis mellifera*–anthophorine bee, hopliine beetle, and short-proboscid nemestrinid fly system found in the winter-rainfall zone *H. pauciflora*, and the anthophorine bee system in such eastern southern African species as *H. baurii*, *H. lactea*, and *H. similis*.

The long-proboscid fly pollination system in *Hesperantha* is, we assume, derived, since it is a more specialized system than those using a wider range of pollinators. The taxonomic distribution of the strategy in the genus makes it clear that it has had multiple origins (Goldblatt, 2003). The eastern southern African species pollinated by *Prosoeca ganglbauri* or *Stenobasipteron wiedemannii* may share a common ancestry. However, the Namaqualand *H. latifolia*, pollinated by *Prosoeca peringueyi*, and the western Karoo *H. oligantha*, inferred to be pollinated by an undescribed *Prosoeca* species, belong to different taxonomic sections of *Hesperantha* (according to Goldblatt, 1984, 2003). Long-proboscid fly pollination is also inferred for two apparently unrelated species of *Hesperantha* sect. *Radiata*, the eastern Cedarberg *H. elsiae* and the southern Cape *H. muirii*, based on flowers with an elongate perianth tube and pink coloration. These two species are most likely local derivatives of the widespread *H. radiata*, the nocturnal flowers of which are pollinated by moths. Thus, while we can say little about the origins of moth pollination in *Hesperantha* flowers, it is clear that long-proboscid fly pollination evolved several times in the genus and involves different species of nemestrinid (and possibly tabanid) flies across the range of the genus in southern Africa. This mirrors the pattern in *Gladiolus* (also belonging to the Crocoideae), in which long-proboscid fly pollination may have evolved at least 10 and possibly 12 times in this genus of 165 species in southern Africa (Goldblatt & Manning, 1999; Goldblatt et al., 2001).

The shift to butterfly pollination in red-flowered populations of *Hesperantha coccinea* is unique in the genus. Although butterflies may share this riverine species with long-proboscid flies, it seems likely that only the rare pink-flowered populations, which Occam's razor suggests must be ancestral, are normally pollinated by long-proboscid flies. The red-flowered populations, which extend from the Amatola Mountains in Eastern Cape Province, South Africa, to Zimbabwe, are pollinated largely,

if not exclusively, by a range of large butterflies, including species of Papilionidae and the satyrid *Aeropetes*.

The shift to exclusive hopliine beetle pollination in *Hesperantha vaginata* (and perhaps its close ally *H. karooica*) is likewise unique in the genus, but flowers shared by apid and anthophorine bees and hopliines occur in a few other species of *Hesperantha*, notably *H. pauciflora*. The evolution of a strictly hopliine pollination system is thus not particularly surprising.

In summary, the radiation of pollination systems in *Hesperantha*, a mid-sized genus of subfamily Crocoideae of the Iridaceae, is not unexpected in view of the diversity of pollination systems in most other genera of any size in the subfamily. Each genus, however, appears to exploit the available spectrum of pollinators in different ways and to different degrees. *Ixia* exhibits a remarkable pattern of radiation based on hopliine beetle pollination and secondarily on long-proboscid flies, whereas *Gladiolus* exploits in particular anthophorine bee pollination, with secondary emphasis on long-proboscid flies, Lepidoptera, or passerine birds. *Lapeirousia* has exploited a range of different long-proboscid flies as pollinators, while a few species have flowers adapted for sphinx or other moth pollination, but some species are pollinated by a combination of bees, wasps, and butterflies.

The pattern of radiation in *Hesperantha* shows particularly marked exploitation of long-proboscid fly pollination in eastern southern Africa, where 11 of the 34 species there (Goldblatt, 2003) have flowers that display the typical adaptations for this strategy. In contrast, species of the southern Africa winter-rainfall zone have exploited small moth pollination (or a combination of moths and apid and anthophorine bees) at the expense of most other pollination systems. Hopliine beetle, exclusive anthophorine bee, and long-proboscid fly systems are limited to only a few species there. Some 22 of the 44 species in the winter-rainfall zone have been shown herein, or may confidently be inferred, to have this small settling moth pollination system, often associated with foraging by large anthophorine bees late in the day, a system not otherwise known in the Iridaceae.

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LINEAGE SORTING AND PHYLOGEOGRAPHY IN *LITHOCARPUS FORMOSANUS* AND *L. DODONAEIFOLIUS* (FAGACEAE) FROM TAIWAN[1]

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Abstract

Gene genealogy of the cpDNA *atp*B-*rbc*L noncoding spacer was reconstructed to assess the phylogeographic pattern of two closely related oaks, *Lithocarpus formosanus* (Skan) Hayata and *L. dodonaeifolius* (Hayata) Hayata (Fagaceae). High levels of nucleotide and haplotype diversities but low levels of genetic differentiation between species and among populations were detected. The result is consistent with the paraphyly of this cpDNA spacer in both species suggested by a neighbor-joining analysis. A minimum spanning network of the cpDNA haplotypes identified two major clades, A and A′ (consisting of clades of B, C, and D). No clades were confined to either species or single populations. Clades B and C did not occur in two smaller populations of *L. dodonaeifolius*. The apportionment of haplotypes between species and populations indicated a lineage sorting of the cpDNA noncoding spacer. On the contrary, RAPD fingerprints revealed limited ongoing gene flow and significant genetic differentiation between species and among populations. Given low possibilities that seeds disperse across a long geographic range in the modern vegetation, high *Vm* values, estimates of number of migrants per generation deduced from the seed-carried organelle DNA marker are likely to represent historical migrations. A migrant-pool model explains the heterogeneous composition of the organelle DNA within populations and the low differentiation among populations. According to geological evidence, during the deglaciation period common ancestral populations were possibly forced to migrate into refugia at local peaks. Invading and adapting to habitats of different elevations, two oaks flower with a lag interval of about half a month, which may have triggered the reproductive isolation and speciation. Ancestral polymorphic alleles, however, prolonged the lineage sorting period within populations and species. Given a relatively short evolutionary duration since isolation, high genetic heterogeneity has made the attainment of coalescence improbable.

Key words: Fagaceae, lineage sorting, *Lithocarpus*, phylogeography, Taiwan.

One of the recent developments in plant evolutionary study is the application of phylogeography to the analysis of evolutionary events (cf. Avise, 1999). Phylogeography uses gene genealogies, which trace phylogenetic relationships among alleles within or among species, in a geographical context (Schaal, 2000). In the past, phylogeographic patterns of many taxa that evolved through glacial cycles or vicariance events have been well demonstrated based on genealogical information of organelle DNA (e.g., *Pinus*, Latta & Mitton, 1997; *Abies*, Tsumura & Suyama, 1998; *Cycas*, Huang et al., 2001; *Fagus*, Demesure et al., 1996; *Quercus*, Petit et al., 1997; *Alnus*, King & Ferris, 1998; *Kandelia*, Chiang et al., 2001; and *Beta*, Desplanque et al., 2000).

High levels of genetic variation were usually detected in these species, in part due to their long evolutionary history. However, the distribution of genetic diversity varies widely between plant species. In contrast to the distinctness between species descending from remote common ancestors (e.g., *Quercus* sects. *Lobatae* and *Cerris*, Manos et al., 1999), low genetic differentiation of organelle DNAs between closely related species has been frequently encountered (e.g., *Ipomopsis*, Wolf et al., 1997; *Quercus*, Dumolin-Lapègue et al., 1999; *Abies*, Tsumura & Suyama, 1998). Lineage sorting, as a result of a short period for coalescence, contributed to the low level of differentiation (Chiang, 2000). Nevertheless, Manos et al. (1999) showed that monophyly of organelle DNA haplotypes could be attained in some recently evolving species. In their study, cpDNA of *Quercus tomentella* (sect. *Protobalanus*) was proved monophyletic, while its most related con-sectional species *Q. cedrosensis*, as well as most other species, remained paraphyletic. Processes such as fluctuation in population size, gene migration, and selection affect the genealogical relationships among haplotypes (Schaal,

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2000). In general, coalescence of neutral alleles (such as noncoding spacers) of maternally inherited organelle DNAs (Rebound & Zeyl, 1994) is regulated by duration of isolation, population number and size, and other evolutionary agents, such as migration (cf. Hoelzer et al., 1998).

In contrast to the research frequently carried out in species of continents or oceanic islands (e.g., Hawaii, Stuessy & Ono, 1998), less attention has been paid to plants of continental islands (e.g., *Abies*, Tsumura & Suyama, 1998; *Cunninghamia*, Lu et al., 2001), which had been a part of the adjacent mainland before geographical separation. Compared to taxa of European and American continents, the distribution of most plants on a continental island such as Taiwan is constrained due to its small area and rugged landscape. In addition, in the last decades, many species of lowland areas have been under threat because of habitat destruction, a result of human economic activities. The effect of random genetic drift could be a more important factor in those island plants with reduced population sizes. Then, low levels of genetic variation within species would be expected.

To understand phylogeographic patterns and the gene genealogy of species of continental islands, oaks provide ideal material. A great number of data are available for species of continents of Europe and North America (Whittemore & Schaal, 1991; Manos et al., 1999), and the fagaceous plants share similar breeding systems and demography. In Taiwan, *Lithocarpus* species are highly diverged, with 14 species recognized (Yang et al., 1997). Like many endemic species that survived glacial cycles on the island, a large number of relictual *Lithocarpus* species, such as *L. castanopsisifolius* (Hayata) Hayata and *L. konishii* (Hayata) Hayata, are sporadically distributed with limited population sizes, partly due to biogeographic history and recent human disturbance (Lin, 1966). The taxonomy of Taiwan's oaks has been well documented (Liao, 1996; Huang et al., 1999). Some species complexes have long puzzled taxonomists, including *Lithocarpus formosanus* (Hayata) Hayata and *L. dodonaeifolius* (Hayata) Hayata. Kudô (1931: 387) recognized the latter within *L. formosanus* (as *Synaedrys* [: *Lithocarpus*] *formosana* fo. *dododaeifolia*), and Li (1953) also suggested a conspecific relationship. In contrast, recent taxonomic treatments (Liao, 1996; Yang et al., 1997) recognized two separate species.

Trees of 4–9 m in height from both taxa in *Lithocarpus* share entire leaf margins and a rounded leaf apex. The oblanceolate leaf shape of *Lithocarpus dodonaeifolius* is distinct from the elliptic leaf shape of *L. formosanus*. In addition, shorter petioles (4–8 mm), longer infructescence (3–5 cm), and tawny tomentose cupule bracts characterize *L. dodonaeifolius*, while longer petioles (10–13 mm), shorter infructescence (ca. 3 cm), and gray tomentose cupule bracts occur in *L. formosanus*. *Lithocarpus formosanus* and *L. dodonaeifolius* are allopatrically distributed in southern Taiwan about 30 km apart. A single extant population of *L. formosanus*, consisting of no more than 100 plants, remains in the wild, although several scattered populations were previously recorded (cf. Lu, 1996). This population is distributed along the Nanjen Stream in the Kengting National Park. Two subpopulations of *L. formosanus* occurring along ridges about 400 m alt. are separated by the Nanjen stream. In contrast, three populations of *L. dodonaeifolius* are distributed along the Central Mountain Range of the Taiwanese island: Mt. Weiliaoshan (with about 100 individuals, ca. 1200 m alt.), Chingshuiying (with about 200 individuals, ca. 1500 m alt.), and Dazen (with 9 individuals, ca. 600 m alt.). These three populations of *L. dodonaeifolius* are isolated by distances between 20 km and 60 km. Ecologically, both species usually grow on wind-facing slopes, mixing with other species of Fagaceae and Lauraceae in tropical or subtropical forests.

Organelle DNA is maternally inherited in oaks (Dumolin et al., 1995) and can only migrate across populations via seed dispersal. An "isolation by distance" model would be expected in oaks, whose seed dispersal is constrained by the migratory capability of the seed carriers. In addition, as a result of stochastic drift, coalescence of cpDNA alleles in populations with small size can be possibly reached. Nevertheless, both ongoing gene flow and historical migratory events have influenced the amount of genetic variation between and within species/populations. In this study, we looked into the stage of lineage sorting of the chloroplast DNA locus at a noncoding spacer located between *atp*B and *rbc*L genes between and within the two endemic *Lithocarpus* species. One population is limited in both population size and number, while the other possesses relatively healthy population structure. Based on genealogical relationships among alleles of the cpDNA locus, the phylogeographic pattern of the Taiwan's *Lithocarpus* species was reconstructed.

In order to determine the level of ongoing gene flow between populations, RAPD fingerprints, which are mostly amplified from the nuclear genome (Hawkins & Harris, 1998), were utilized to assess the extent of migration. In the study, several objectives are pursued: (1) the partitioning pattern of cpDNA variation within and between species; (2)

the possible migratory mode of Taiwan's oaks over the geological history; (3) the coalescence process of cpDNA alleles within species and populations; and (4) the level of ongoing gene flow between populations.

Materials and Methods

Population samples

A single population of *Lithocarpus formosanus* and three populations of *L. dodonaeifolius* were surveyed (Table 1). Geographically, these populations are 20–95 km apart. Except for the complete sampling in the Dazen population of nine, about 10% of wild individuals were sampled randomly (Table 1). Both species of *Lithocarpus* grow on the wind-facing slopes. Young and healthy leaves were collected in the field, rinsed with tap water and dried in silica gel. Voucher specimens were deposited at NCKU at Cheng-Kung University. All samples were stored at −70°C until they were processed.

DNA extraction, PCR, and nucleotide sequencing

Genomic DNA was extracted from *Lithocarpus* leaf tissues following the CTAB procedure (Murray & Thompson, 1980). PCR amplification was carried out in a 100 μL reaction using 10 ng of template DNA, 10 μl of 10× reaction buffer, 10 μl $MgCl_2$ (25 mM), 10 μl dNTP mix (8 mM), 10 pmole of each primer, 10 μl of 10% NP-40, and 2 U of *Taq* polymerase (Promega, Madison, Wisconsin, U.S.A.). The reaction was programmed on an MJ Thermal Cycler (PTC 100) as one cycle of denaturation at 95°C for 4 min., 30 cycles of 45 sec denaturation at 92°C, 1 min. 15 sec. annealing at 52°C, and 1 min. 30 sec. extension at 72°C, followed by 10 min. extension at 72°C. Template DNA was denatured for 4 min. (first cycle), and cooled on ice immediately. A pair of universal primers for cpDNA *atp*B-*rbc*L spacer (Chiang et al., 1998), dNTP, and *Taq* polymerase were added to the above ice-cold mix. Reaction was restarted at the first annealing at 52°C.

PCR products were purified by electrophoresis in 1.0% agarose gel using 1 × TAE buffer. The gel was stained with ethidium bromide, and the desired DNA band was cut and eluted using agarose gel purification (QIAGEN). Eluted PCR products were directly sequenced in both directions by standard methods of the *Taq* dye deoxy terminator cycle sequencing kit (Perkin Elmer) on an Applied Biosystems Model 377A automated sequencer (Applied Biosystems).

Sequence alignments and phylogenetic analyses

Nucleotide sequences of *atp*B-*rbc*L noncoding spacer of cpDNA were registered with EMBL (Table 1). Nucleotide sequences were aligned with the program Genetics Computer Group (GCG) Wisconsin Package (Version 10.0, Madison, Wisconsin) and later adjusted visually. Neighbor-joining (NJ) analysis, calculating Kimura's (1980) two-parameter distance and excluding the gaps, was performed using software MEGA (Kumar et al., 1993). Confidence of each reconstructed clade was tested by bootstrapping (Felsenstein, 1985) with 1000 replicates using unweighted characters. The nodes with bootstrap values greater than 0.70, as a rule of thumb, are significantly supported with ≥ 95% probability (Hillis & Bull, 1993). The number of mutations between haplotypes in pairwise comparisons, calculated using "number of differences" implemented in MEGA (Kumar et al., 1993), was used to construct a minimum spanning network with the aid of the MINSPNET (Excoffier & Smouse, 1994) in an hierarchical manner (Chiang & Schaal, 1999). After linking the related haplotypes into a clade, closely related clades were linked further to form higher level groups and thereby a network.

RAPD fingerprint analysis

We used the polymerase chain reaction (PCR) with arbitrary primers for obtaining RAPDs following Williams et al. (1990). We used 5 ng of DNA template, 0.3 μM primer (Operon Technologies, Alameda, California), 1 unit of Taq polymerase (Promega), 2.5 μL of PCR buffer, 2.5 mM $MgCl_2$, and 100 μM of each dNTP for each 25 μL PCR reaction, respectively.

PCR amplification took place in a PTC-100 thermal cycler (MJ Research Inc.) programmed for an initial 3 min. denaturation at 94°C, 35 cycles of 20 sec. at 94°C, 30 sec. at 36°C, and 90 sec. at 72°C, followed by a 10-min. final extension at 72°C. Forty 10-base oligonucleotide primers were screened from the Operon (Alameda, California) K and N series (OPK-01~OPK-20; OPN-01~OPN-20). RAPD products were electrophoresed on 2% Nusieve 3:1 agarose gels, stained by ethidium bromide, and photographed with Polaroid type 667 film.

A RAPD data matrix based on the presence and absence of loci was prepared by the aid of AMOVA-PREP (version 1.01; Miller, 1998). We used AMOVA version 1.55 (Excoffier et al., 1992) to deduce the significance of geographical divisions both between populations and between regions. The statis-

Table 1. Localities sampled within each species and population of Taiwan oaks. The number of individuals sampled and sequenced is indicated. Haplotype diversity (H), nucleotide diversity (*Dij*), and minimum recombination events (Rm) are indicated. H = the average number of sequence differences. *Dij* = the average number of nucleotide differences.

Species	Location	Coordinate	Symbol	Sample size	Haplotype diversity (H)	Nucleotide diversity (*Dij*) %	Chlorotypes	Minimum recombination events (Rm)	EMBL accession number
L. formosanus	Wanlider	120°51′E, 22°03′N	for	19	1	8.074 ± 1.149	A, B, C	4	AJ390792–AJ390810
L. dodonaeifolius				39	1	6.026 ± 0.702	A, B, C, D	15	
	Chingshuiying	120°45′E, 22°22′N	doda	19	1	7.039 ± 0.545	A, B, C, D	8	AJ252218, AJ252221–AJ252223 AJ252230–AJ252234 AJ390818–AJ390822, AJ390827 AJ390831–AJ390832 AJ390835–AJ390836
	Dazan	120°48′E, 22°16′N	dodb	9	1	4.560 ± 2.224	A, D	5	AJ252217, AJ252227–AJ252229 AJ390829–AJ390830 AJ390833–AJ390834, AJ390837
	Weiliaoshan	120°40′E, 22°52′N	dodc	11	1	4.554 ± 1.690	A, D	8	AJ252216, AJ252219–AJ252220 AJ252224–AJ252226 AJ390823–AJ390826, AJ390828

tics of molecular variants ΦCT (among regions), ΦST (among populations), and ΦSC (among populations within a region) were estimated (cf. Chiang et al., 2001). The significance of these F-statistic analogues was evaluated by 1000 random permutations. The UPGMA dendrogram of populations was drawn based on pairwise dissimilarities using software TFPGA (version 1.3; Miller, 1997).

POPULATION GENETIC ANALYSIS OF THE cpDNA AND mtDNA SEQUENCE VARIATION

Levels of inter- and intra-population genetic diversity were quantified by indices of haplotype diversity (h) (Nei & Tajima, 1983) and pairwise estimates of nucleotide divergence (Dij) (Jukes & Cantor, 1964) using DnaSP (Version 3.0, Rozas & Rozas, 1999). Patterns of geographical subdivision and gene flow were also estimated hierarchically with the aid of DnaSP. Recombination and gene conversion events were detected using DnaSP. Gene flow within and among regions (populations) was approximated as Nm, the number of female migrants per generation between populations. It was estimated using the expression FST = 1/(1 + 2 Nm), where N is the female elective population size and m is the female migration rate (Slatkin, 1993).

The pattern of "isolation by distance" was assessed in both cpDNA and RAPD data by plotting pairwise genetic distance (for RAPD) or log (Nm) values (for cpDNA) against log (geographical distance) (cf. Slatkin, 1993; Forcioli et al., 1998; Stauffer et al., 1999). The significance of the association between Nm and geographical distance was determined by a regression F test using the SPSS program (Norusis, 1994).

RESULTS

HAPLOTYPES, NUCLEOTIDE DIVERSITY, AND cpDNA PHYLOGENY OF *LITHOCARPUS FORMOSANUS* AND *L. DODONAEIFOLIUS*

In this study, the *atp*B-*rbc*L noncoding spacer of cpDNA in *Lithocarpus formosanus* and *L. dodonaeifolius* were PCR amplified and sequenced. Length of the *atp*B-*rbc*L spacer of cpDNA varied from 730 bp (isolate *doda36*) to 935 bp (isolate *for4005*). A total of 996 bp were aligned (alignment available from authors on request), of which 201 sites (20.2%) excluding the sites with alignment gaps were polymorphic. This noncoding spacer was A+T rich (68.8%). All sequences were unique. Nineteen haplotypes (h = 1.0) and 39 haplotypes (h = 1.0) of the cpDNA noncoding spacer were determined in *L. formosanus* and *L. dodonaeifolius*, respectively, according to the DnaSP analyses. Nucleotide diversity (Jukes & Cantor, 1964) of 0.08074 ± 0.01149 and 0.06026 ± 0.00702 was estimated in the above species, respectively. In the largest population (Chingshuiying) of *L. dodonaeifolius*, nucleotide diversity as measured by pairwise estimates (Dij = 0.07039 ± 0.00545) of the cpDNA was higher than that of those smaller populations (Dij = 0.04560 ± 0.02224 for Dazen and Dij = 0.04554 ± 0.01690 for Weiliaoshan) (Table 1).

A neighbor-joining (NJ) tree was reconstructed based on the genetic distance among aligned sequences of the cpDNA. Four groups (A–D) were identified and supported by bootstrap significantly (Fig. 1). Clades B and C were grouped further, although not significantly (bootstrap value = 0.52). The monophyly of the cpDNA noncoding spacer in either *L. formosanus* or *L. dodonaeifolius* was not suggested by the NJ analysis. Nevertheless, clade D consisted of individuals of *L. dodonaeifolius* exclusively (Table 1). Within clade A, most sequences of *L. formosanus* and *L. dodonaeifolius* were mixed, except for a subcluster A^+, which comprised sequences of the latter species only. Within the clade B, an unusually long branch leading to the *for1502* (*L. formosanus*) was identified, which differed by 49 mutational changes from its closest sequence of *for1501* (*L. formosanus*) (Fig. 2).

GENETIC DIFFERENTIATION BETWEEN *LITHOCARPUS FORMOSANUS* AND *L. DODONAEIFOLIUS*

A minimum spanning network was constructed based on mutational changes between sequences (Fig. 2). Paraphyly of the cpDNA noncoding spacer in both species agrees with the conventional cladistic analysis. Two major lineages with 98 mutational changes were determined, i.e., A and A′. Within clade A, several ancestral haplotypes nested in the network as interior nodes were identified: isolates *for203* representing *Lithocarpus formosanus*, and *doda20*, *doda1715*, *dodb008*, *dodb009*, *dodb004* for *L. dodonaeifolius*, indicating shared ancestral polymorphisms and nearly equal age of the two species. Clade B is linked to *doda20* (*L. dodonaeifolius*) via *for3903* (*L. formosanus*). Within the second clade A′, clade B is linked to clade C with 25 mutational changes, and clade D is linked to clade C with 20 mutational changes.

Low genetic differentiation of the cpDNA locus was detected between *Lithocarpus formosanus* and *L. dodonaeifolius*. An Nm of 43.75 and an FST of 0.00575 were deduced. Pairwise comparisons be-

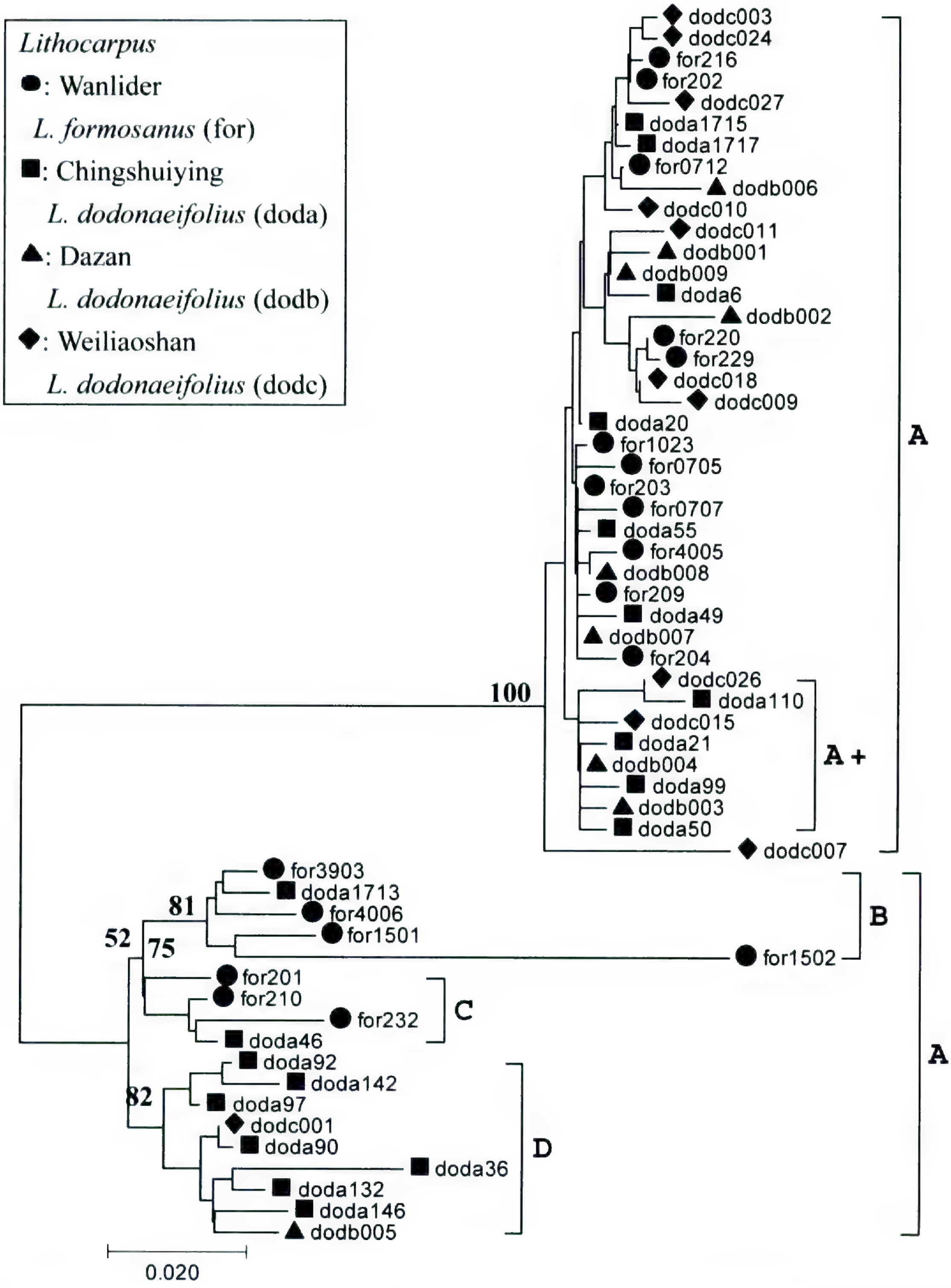

Figure 1. Neighbor-joining (NJ) tree of cpDNA of *Lithocarpus formosanus* and *L. dodonaeifolius*. Numbers in bold at nodes indicate bootstrap values. Four clades (A–D) and subtype A⁺ are indicated.

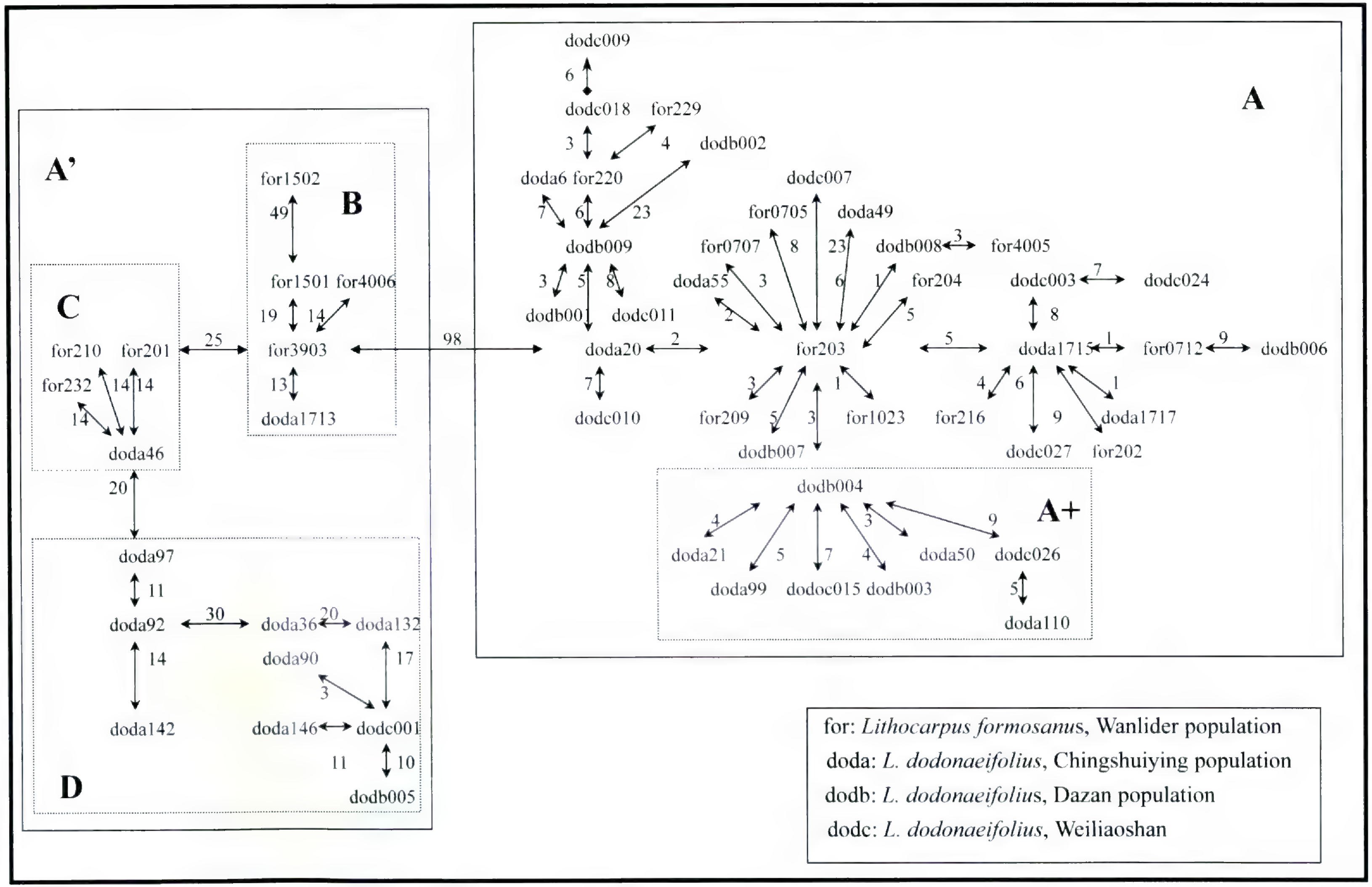

Figure 2. Minimum spanning network for two *Lithocarpus* oaks from Taiwan based on the mutational changes between cpDNA haplotypes. Clades A and A′ (consisting of B–D) were indicated. Numbers at the nodes indicate the steps of mutations.

Table 2. Pairwise *Nm* (above the diagonal) and Fst (below the diagonal) among populations deduced from chloroplast DNA sequences. For symbols for populations see Table 1. *Nm* refers to the number of female migrants per generation between populations. Fst = $1/(1+2Nm)$, where N = female effective population size, m = female migrant rate.

	L. formosanus	*L. dodonaeifolius*			
	for		doda	dodb	dodc
L. formosanus for		43.74	126.89	3.14	2.34
L. dodonaeifolius	0.00575				
doda		0.00197		1.49	1.22
dodb		0.07365	0.1439		4.65
dodc		0.09638	0.1390	0.05679	

tween *L. formosanus* with each population of *L. dodonaeifolius* also indicated high *Nm* values, ranging from 2.34 to 126.89, and low Fst, ranging from 0.00197 to 0.09638 (Table 2). Between populations of *L. dodonaeifolius*, the deduced *Nm* ranged from 1.22 to 4.65 and the deduced Fst ranged from 0.05679 to 0.1439. Subpopulations of *L. formosanus*, which are separated by a stream, were not differentiated based on a high value of deduced *Nm* (40.50) and low Fst (0.01250).

When lineages A and A′ were considered separately, within *L. formosanus*, both lineages were differentiated significantly, with an *Nm* of 0.11 and an Fst of 0.6937 (Table 3). Low differentiation between *L. formosanus* and each population of *L. dodonaeifolius* was suggested based on the high deduced *Nm* of the clade A (with a range of 6.83–57.29). In contrast, the much lower deduced *Nm* of the lineage A′ between *L. formosanus* and populations of *L. dodonaeifolius* was obtained, with a range between 0.06 and 2.06. Within *L. dodonaeifolius*, clade A was not differentiated between populations according to the high deduced *Nm*, with a range of 13.64 to 1015.96, while significant differentiation between populations was detected in the clade A′ based on the low deduced *Nm* (0.00–0.42). In addition, the nucleotide diversity is higher as measured by pairwise estimates in the A′ clade ($Dij = 0.04549 \pm 0.02237$) than in the A clade ($Dij = 0.01637 \pm 0.01335$).

Based on DnaSP analysis of sequences of both species as a whole, 18 possible minimum recombination events were detected. Four and 15 minimum recombination events occurred in *L. formosanus* and *L. dodonaeifolius*, respectively. In contrast to short DNA fragments involved in the

Table 3. Pairwise *Nm* (above diagonal) and Fst (below diagonal) between species and populations with lineages A and A′ considered separately. *Nm* refers to the number of female migrants per generation between populations. Fst = $1/(1+2Nm)$, where N = female effective population size, m = female migrant rate.

	L. formosanus for		*L. dodonaeifolius* doda		dodb		dodc	
	lineage A	lineage A′	lineage A	lineage A′	lineage A	lineage A′	lineage A	lineage A′
L. formosanus for lineage A		0.11	42.21	0.11	6.83	2.24	57.29	0.04
L. formosanus for lineage A′	0.6937		0.07	2.06	0.16	0.06	0.08	0.14
L. dodonaeifolius doda lineage A	0.0059	0.7755		0.07	38.85	1.00	13.64	0.01
L. dodonaeifolius doda lineage A′	0.7041	0.1081	0.7894		0.13	0.05	0.07	0.42
L. dodonaeifolius dodb lineage A	0.0380	0.6129	0.0064	0.6549		2.30	1015.96	0.06
L. dodonaeifolius dodb Lineage A′	0.1003	0.8193	0.2000	0.8453	0.0981		1.00	0.00
L. dodonaeifolius dodc Lineage A	0.0044	0.7464	0.0180	0.7728	0.0003	0.2000		0.02
L. dodonaeifolius dodc Lineage A′	0.8766	0.6351	0.9486	0.3716	0.7992	1.000	0.9126	

genetic recombination in *L. dodonaeifolius*, two large DNA fragments, i.e., fragments of (261, 563) and (831, 950), were identified in *L. formosanus* based on DnaSP analyses (Table 1).

RAPD FINGERPRINTS AND GENE FLOW

A UPGMA dendrogram was constructed based on the deduced genetic distance among individuals (Fig. 3). All individuals of *L. formosanus* were grouped together, as were those of *L. dodonaeifolius*. Individuals of the Dazen population as well as the Weiliaoshan population were clustered together, both of which were nested within the group of the Chingshuiying population. The UPGMA dendrogram (Fig. 4) based on the TFPGA analysis, which recognized each population (instead of individual) as a unit, suggested significant differentiation, with about 54.8% dissimilarity, between *L. formosanus* and *L. dodonaeifolius*. In addition, within *L. dodonaeifolius* populations from Weiliaoshan and Dazen shared highest similarity (about 85%). Based on the deduced *Nm* (1.06) and Fst (0.19149), estimating the gene flow, the subpopulations of *L. formosanus* were barely differentiated.

Discussion

GENETIC VARIABILITY OF THE NONCODING SPACER BETWEEN *atp*B AND *rbc*L GENES OF cpDNA IN TAIWANESE OAKS

Lithocarpus formosanus and *L. dodonaeifolius* seemed to possess higher levels of cpDNA haplotype diversity (19 and 39 haplotypes, respectively; Table 1) than other plants, e.g., 13 cpDNA haplotypes in *Beta vulgaris* subsp. *maritima* (Desplanque et al., 2000), 11 haplotypes in *Argania* (El Mousadik & Petit, 1996), 23 haplotypes in white oaks (Dumolin-Lapègue et al., 1997), and 13 haplotypes in *Alnus* (King & Ferris, 1998). The nucleotide diversity ($Dij = 0.06026$ and $Dij = 0.08074$) of these two Taiwanese oaks was also high, compared to that of California pines ($Dij = 0.003 \pm 0.002$) (Hong et al., 1993).

High level of genetic diversity in the Fagaceae (cf. Petit et al., 1997; Dumolin-Lapègue et al., 1997) is probably associated with their long evolutionary history, which allows genetic variation to accumulate within lineages (cf. Chiang & Schaal, 1999). Nevertheless, the higher haplotype diversity of cpDNA of *Lithocarpus* from Taiwan may be simply derived from different molecular techniques employed. Nucleotide sequencing usually detects a higher level of genetic variation than do the RFLP and PCR-RFLP techniques. In our analysis, according to the deduced restriction site map, only four chlorotypes (cpDNA polymorphisms) for 58 individual haplotypes could be identified. Within smaller populations of *L. dodonaeifolius* from Weiliaoshan and Dazen, the number of major clades was even lower (with only two), while high levels of haplotype diversity ($h = 1$) and nucleotide diversity ($Dij = 0.045$–0.046) were assessed based on the sequence variation. As stated by Desplanque et al. (2000), a substantial within-population diversity in natural plants should have existed (cf. McCauley, 1994; El Mousadik & Petit, 1996; Raspe, 1998). The detection of the existing variation surely depends not only on the conservative nature of the molecular marker itself, but also the sensitivity of the tools employed. In this study, the so-called "higher" level of genetic variation of *L. formosanus* and *L. dodonaeifolius* turned out much lower than that of other species, when nucleotide sequences were transferred to RFLP data (data not shown). Such low level of chlorotype diversity, as expected, may be ascribed to their smaller population number and size.

Interestingly, *Lithocarpus formosanus* possessed a much higher level of nucleotide diversity than did *L. dodonaeifolius*, despite fewer chlorotypes (three types) existing in the former species (vs. four types for *L. dodonaeifolius*). In general, populations with larger sizes maintained higher genetic variation compared to smaller ones, such as Chingshuiying ($Dij = 0.07039$) versus Dazen ($Dij = 0.04560$) and Weiliaoshan ($Dij = 0.04554$). According to the longest branch of the *for1502* ($P < 0.05$) in the neighbor-joining tree (Fig. 1), the unusually high nucleotide diversity in *L. formosanus* was probably ascribed to the most diverged sequence. When the sequence of *for1502* was removed from the calculation, a low level of nucleotide diversity ($Dij = 0.07369 \pm 0.01161$) was obtained. This deviation from a molecular clock ($P < 0.01$) can hardly be attributable to natural selection, whose effect is usually not intense on a noncoding spacer (Graur & Li, 2000). According to the DnaSP analysis, random genetic recombination within the chloroplast DNA marker may have resulted in the long branch of *L. formosanus* (cf. Huang et al., 2001).

As a noncoding region, the *atp*B-*rbc*L spacer has relatively low functional constraints. With nearly neutral evolution, mutations to some extent would have been retained within each lineage. However, extremely low substitution rates in the *atp*B-*rbc*L spacer have been detected in other plants (Manen & Natali, 1995; Chiang & Schaal, 2000a, b). High levels of genetic variation of the cpDNA of *Lithocarpus* in Taiwan may be in part ascribed to fre-

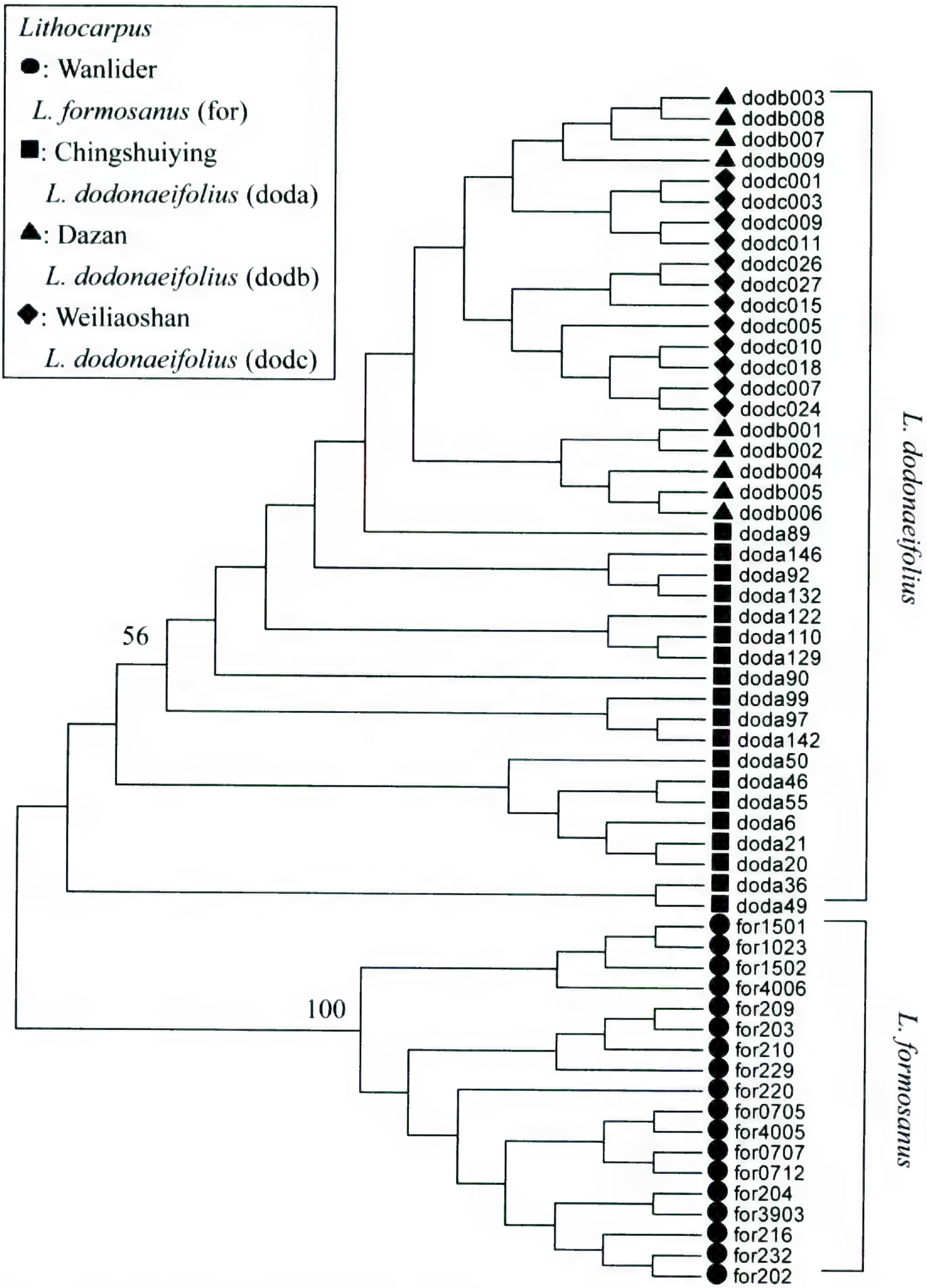

Figure 3. UPGMA tree of individuals of *Lithocarpus formosanus* and *L. dodonaeifolius* based on RAPD data. Numbers at nodes indicate bootstrap values.

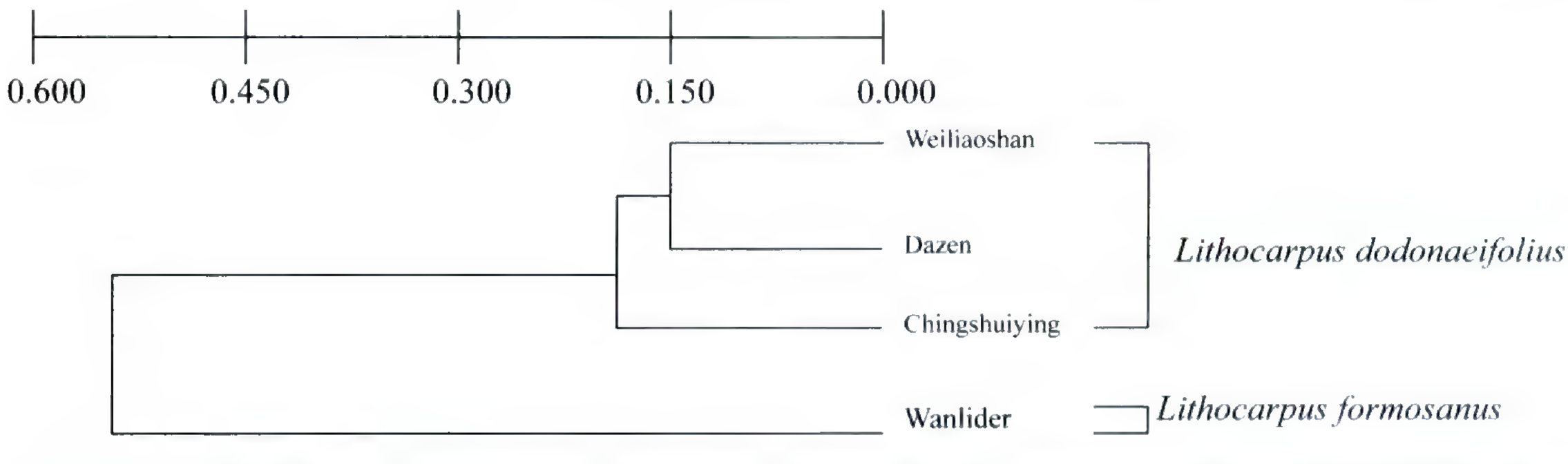

Figure 4. UPGMA tree of populations of *Lithocarpus formosanus* and *L. dodonaeifolius* based on RAPD data for: *L. formosanus* at Wanlider; doda: *L. dodonaeifolius* at Chingshuiying; dodb: *L. dodonaeifolius* at Dazen; dodc: *L. dodonaeifolius* at Weiliaoshan. The level of dissimilarity between populations is indicated.

quent intramolecular recombination, a process well documented in plant organelle DNAs (e.g., Stern & Palmer, 1984; Yesodi et al., 1997; Senda et al., 1998; Huang et al., 2001). Large DNA fragments involved in the intramolecular recombination of the cpDNA may have contributed to the longer branch leading to the *for1502*. Indel events were responsible for high polymorphisms of cpDNA as well. In contrast to random genetic recombination, indel events occurring in bp positions between 311 to 608 for the *atp*B-*rbc*L noncoding spacer appeared nonrandom.

PHYLOGEOGRAPHY OF *LITHOCARPUS FORMOSANUS–L. DODONAEIFOLIUS* AND GENE GENEAOLOGY OF cpDNA

RAPD fingerprints revealed significant differentiation between *Lithocarpus formosanus* and *L. dodonaeifolius* based on the UPGMA dendrogram and deduced FST. Genetic distance between populations is strongly associated with geographical distance ($P < 0.05$, Fig. 5A), which is consistent with a model of isolation by distance (Slatkin, 1993). Interestingly, according to the differentiation between subpopulations of *L. formosanus* on the UPGMA dendrogram (Fig. 3), a ravine of narrower than 1 km in width (i.e., Nanjen stream) may become a natural barrier for pollen dispersal, although it is not significant.

In contrast to the significant genetic differentiation between species and populations indicated by RAPD fingerprinting, which represents the level of ongoing gene flow between populations, the cpDNA noncoding spacer within species and populations was non-monophyletic. The most common chlorotype A (68.9%) was predominant over other alleles (8.6% for B, 6.9% for C, and 15.6% for D) and was widespread in all populations. In contrast, chlorotype D was exclusive to *Lithocarpus dodonaeifolius*, while chlorotypes B and C were distributed in *L. formosanus* and the Chingshuiying population of *L. dodonaeifolius*. The biased distribution of alleles in populations plus low differentiation between species suggested lineage sorting of the cpDNA locus in both *Lithocarpus* species (cf. Hoelzer et al., 1998; Young, 1998). Lineage sorting results from a process of differentiated births and deaths, when ancestral polymorphisms are passed down to descendent lineages (populations) (cf. Futyuma, 1998; Chiang, 2000). It usually blurs the inference of organismal phylogeny. In this study, monophyly of the chlorotype D at species level, i.e., within *L. dodonaeifolius*, and paraphyly of other chlorotypes indicated that these chlorotypes are at different lineage sorting periods.

The extent of lineage sorting is usually determined by the genetic heterogeneity within populations and the migratory mode, which in turn is associated with the ongoing gene flow and natural hybridization as well as geological history that the species evolved through. Recurrent introgression is typically invoked to explain such sorting (cf. Manos et al., 1999). However, unexpectedly high *Nm* values between species and populations deduced from the nucleotide sequences of the cpDNA locus of *Lithocarpus* in Taiwan and the low correlation between *Nm* (up to 126.89) and the geographic distance ($P > 0.05$, Fig. 5B) indicates that the migratory mode may have deviated from the stepping-stone model, Wright's island model, or an isolation-by-distance model (cf. Hamrick & Nason, 1996).

Evidently, given limited pollen dispersal among populations (indicated by our RAPD results), the migration of *Lithocarpus* fruits or nuts across a geographic range of 20–95 km in modern habitats is even more improbable due to the discontinuity of vegetation and the constraint of migratory capabilities of any fruits- or nuts-carrying animals. Although some low levels of incidental seed dispersal among populations cannot be simply ruled out, un-

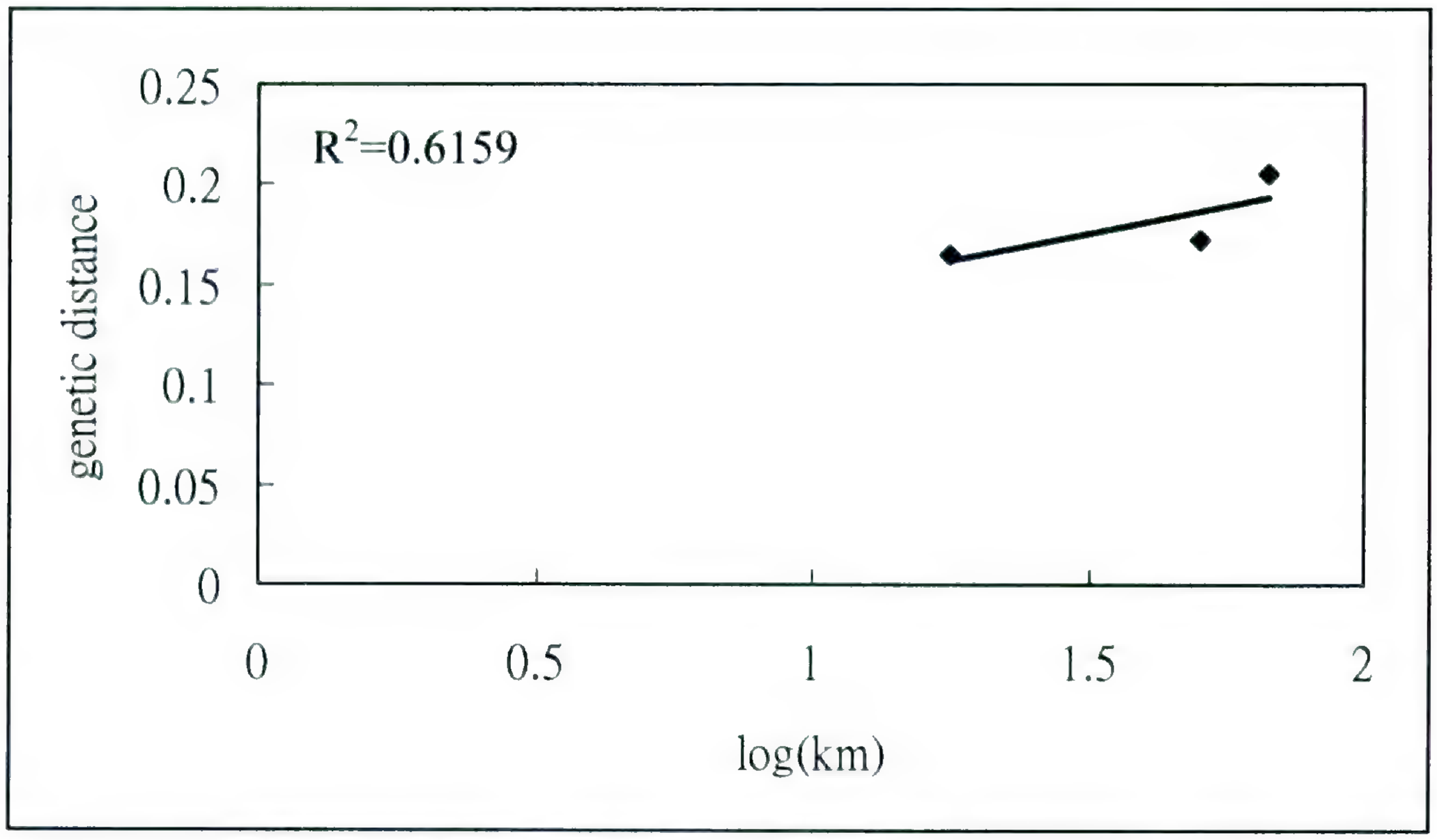

Figure 5. —A. Scatterplot of genetic distance and logarithmic scales of geographic distance among populations of *L. dodonaeifolius* based on RAPD data. Regression statistics: $R^2 = 0.6159$, $P < 0.05$. —B. Scatterplot of logarithmic scales of *Nm* and geographic distance among populations of *Lithocarpus formosanus* and *L. dodonaeifolius* based on chloroplast DNA variation. Regression statistics: $R^2 = 0.0091$, $P > 0.05$. N = female effective population size, m = female migrant rate.

usually high *Nm* values are likely to represent historical migration events instead of the current gene flow. Low genetic differentiation due to shared and heterogeneous composition of organelle DNAs within each population and the high deduced *Nm* between populations suggested a migrant-pool model, a migratory pattern with colonists recruited from a random sample of all the other populations (Wade & McCauley, 1990). Usually this model is associated with glaciation or vicariance events, which ac-

cording to fossil evidence may disturb the vegetation dramatically at a large geographic scale.

Like many angiosperm species (e.g., Fagaceae, Ferris et al., 1995, Petit et al., 1997, Dumolin-Lapègue et al., 1997; beeches, Koike et al., 1998; and beets, Desplanque et al., 2000) and gymnosperms, such as *Cunninghamia* (Lu et al., 2001) as well as *Pinus* (Strauss et al., 1993), oaks survived glacial cycles (cf. Bennett, 1990; Huang et al., 2001). According to geological record, since the late Pleistocene, Taiwan was the southeastern edge of the Asian continent before the formation of Taiwan Strait about 100,000 BP (Lin, 1966; Tsukada, 1966; Kizaki & Oshiro, 1977). This continental island was linked to the mainland via a land bridge and was not completely isolated until the last glacial retreat ca. 18,000 to 20,000 BP (Lin, 1966). Geological evidence indicates that ice ages have occurred at regular intervals of approximately 100,000 years followed by warm periods of about 20,000 years (Milankovitch cycles) (cf. Bennett, 1990; King & Ferris, 1998). During the glacial maximum many oaks and conifers previously dominant in the northern part of eastern Asia were forced to migrate into refugia in southern China and Taiwan (Chiang et al., 1999), which were mostly distributed at low elevations (cf. Tsukada, 1966). During the subsequent deglaciation, elevated global temperatures forced the lowland plants to migrate to high elevations or local peaks. Pollen records reveal the migration routes of many relictual and endemic species, which constitute a large portion of Taiwan's flora (Shaw, 1997). The current geographical distribution of *Lithocarpus dodonaeifolius* and *L. formosanus* is possibly a result of such a migration history.

According to the shared cpDNA alleles of the *atp*B-*rbc*L noncoding spacer, the speciation of *Lithocarpus dodonaeifolius* and *L. formosanus* may be recent. Like other fagaceous plants, migration via long-range seed dispersal (cf. Petit et al., 1997) of the ancestral populations of the Taiwan oaks became possible due to the dramatic change of vegetation (cf. Chiang & Hong, 1999) during deglaciation. Many novel niches were then available for plants that survived after species extinction. Seeds from different resource populations may have migrated into the refugia and settled subsequently. Such migration may have increased the heterogeneity of cpDNA composition within populations.

Extinction and re-colonization regulated by geological events, however, were thought to enhance genetic differentiation among populations (cf. Wright, 1977) owing to founder events resulting from the colonization by a small number of surviving individuals. Recently, Wade and McCauley (1990) further suggested that the results of extinction/re-colonization on genetic differentiation among populations depend on the number of founders as well as the level of heterogeneity of genetic composition within populations according to coalescence theory. When the colonist size is small and the genetic heterogeneity is low, genetic differentiation among populations will be reached fast via stochastic processes alone.

Despite the relatively small population size in both *Lithocarpus* species, no coalescence has been achieved within populations. To counter the genetic diversity loss within small populations due to genetic drift, it is likely that the genetic composition of ancestral populations, even species, prior to deglaciation as well as succeeding colonizing populations was highly heterogeneous. The four chlorotypes noted for these two *Lithocarpus* species in Taiwan may have existed long before the speciation event. In addition, recurrent genetic recombination within the chloroplast intergenic spacer may have increased the heterogeneity within species as well. Given small population sizes, the low level of genetic differentiation among *Lithocarpus* populations at the cpDNA noncoding spacer region is possibly ascribed to a short duration (since the last deglaciation) for coalescence.

Lineage sorting (or the attainment of monophyly) of chlorotypes within species and populations is assuredly regulated by the stochastic genetic drift (Chiang, 2000). The high frequency of the chlorotype A over others in both *Lithocarpus* species and the high frequency of the chlorotype B in *L. formosanus* (80%) illustrate this random effect. With a short time span for coalescence, monophyly of the cpDNA locus has not been attained within either species. The chlorotype D may have been drifted in *L. formosanus* due to its smaller population size. Obviously, the larger population (200 individuals) at the Chingshuiying site possessed higher genetic variation compared to the other populations of *L. dodonaeifolius*. Low genetic diversity in Weiliaoshan and Dazen populations for *L. dodonaeifolius* is ascribed to the lack of chlorotypes B and C. Deduced *Nm* values seemed to be indicative of lineage sorting in clades A and A′ (Table 3). Lower *Nm* among populations derived from clade A′ relative to clade A indicates a higher level of coalescence, e.g., the fixation of chlorotype D in *L. dodonaeifolius*. Drift of rare chlorotypes in smaller populations (D in *L. formosanus* as well as B and C in Weiliaoshan and Dazen populations of *L. dodonaeifolius*) thereby resulted in higher levels of genetic differentiation and genetic diversity compared to the

widespread and dominant chlorotype A across populations of both species. However, differences of deduced *Nm* values between clades A and A′ revealed problems and limitations with the interpretation of such indirect estimates of gene flow among populations (cf. Bossart & Prowell, 1998).

In contrast to the lineage sorting of the cpDNA locus, RAPD fingerprints attained "coalescence" at most loci and resulted in significant genetic differentiation between species. This coalescence at population level, however, has not been completely reached. Interestingly, subsets of smaller populations from Weiliaoshan and Dazen for *Lithocarpus dodonaeifolius* were nested within the cluster of Chingshuiying individuals, as indicated by the UPGMA tree (Fig. 3). Coherence of smaller populations versus the division seen in RAPD sampling within the larger population indicated such a random coalescence process. Incongruence between organelle DNA and RAPD fingerprints, which are usually amplified from the nuclear genome (Hawkins & Harris, 1998), may derive from the different inheritance modes between the two genomes. Genetic recombination between homologous chromosomes may have played a determining role in homogenizing the genetic differences within demes and thereby increasing the heterogeneity between populations, while crossing-over is usually lacking in organelle DNAs due to its haploid nature.

Accordingly, gene flow between *Lithocarpus dodonaeifolius* and *L. formosanus* may have been blocked since their postglacial resettlement. Adapting to habitats at different elevations as they occur, both *Lithocarpus* flower with a lag interval of about half a month. The reproductive barriers between the two species may be complete. In contrast to many European and American Fagaceae (Whittemore & Schaal, 1991; Howard et al., 1997; Manos et al., 1999; Samuel, 1999), which hybridize naturally when populations are sympatrically distributed, no interspecific hybrids have been reported in these Taiwanese *Lithocarpus*.

CONTINENT-ISLAND DISCREPANCY IN VARIATION ALLOTMENT

At the intraspecific level, patchy structure of local populations (e.g., *Aquilegia*, Strand et al., 1996; Fagaceae, Petit et al., 1997; Dumolin-Lapègue et al., 1999) or geographic subdivision between long isolated populations (e.g., northern and southern populations of *Liriodendron tulipifera* L., Sewell et al., 1996; Sarmathic–Baltic and Alpine–Central European populations of *Picea abies* (L.) H. Karst., Vendramin et al., 2000) have been documented in many tree species of continents. Low level of organelle DNA differentiation among local populations was detected in *Lithocarpus dodonaeifolius* and *L. formosanus* as well as other plants of continental islands, such as *Cycas taitungensis* Shen et al. (Huang et al., 2001), *Amorphophallus* (cf. Chiang & Peng, 1998), *Michelia formosana* (Kanehira) Masamune (Lu et al., 2002) of Taiwan as well as Japanese *Abies* (Tsumura & Suyama, 1998). Due to the limited area and available habitats of the island, the population size of Taiwan's oaks is effectively smaller than that of continental species. Under near neutrality, a long period of lineage sorting for cpDNA chlorotypes in small populations may be likely ascribed to high levels of heterogeneity in genetic composition. Interestingly, greater genetic variation has been noted in southern continental refugia (such as Italy, the Balkans, and the Iberian Peninsula) than in northern populations (e.g., Central Europe) (European oaks, cf. Dumolin-Lapègue et al., 1997, 1998; European *Alnus*, King & Ferris, 1998; *Fagus*, Demesure et al., 1996; and Japanese *Abies*, Tsumura & Suyama, 1998). The continent-island discrepancy may be associated with the fact that Taiwan, which is straddled across today's subtropics to tropics, is much more south than most areas of European and American continents geographically. Taiwan may have provided more fitting habitats for surviving plants during the glacial maximum than mainland refugia.

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CONTENTS

A Revision of *Trisetum*, *Peyritschia*, and *Sphenopholis* (Poaceae: Pooideae: Aveninae) in Mexico and Central America ——— *Victor L. Finot, Paul M. Peterson, Robert J. Soreng & Fernando O. Zuloaga* 1

Revision of *Metastelma* (Apocynaceae–Asclepiadoideae) in Southwestern North America and Central America ——— *Sigrid Liede & Ulrich Meve* 31

A Taxonomic Revision of the *Paeonia anomala* Complex (Paeoniaceae) ——— *Hong De-Yuan & Pan Kai-Yu* 87

Phylogeny of *Smelowskia* and Related Genera (Brassicaceae) Based on Nuclear ITS DNA and Chloroplast *trn*L Intron DNA Sequences ——— *Suzanne I. Warwick, Ihsan A. Al-Shehbaz, Connie A. Sauder, David F. Murray & Klaus Mummenhoff* 99

Phylogenetic Relationships of *Vulpia* and Related Genera (Poeae, Poaceae) Based on Analysis of ITS and *trn*L-F Sequences ——— *Pedro Torrecilla, José-Angel López-Rodríguez & Pilar Catalán* 124

Geographical Diversification of Tribes Epilobieae, Gongylocarpeae, and Onagreae (Onagraceae) in North America, Based on Parsimony Analysis of Endemicity and Track Compatibility Analysis ——— *Liliana Katinas, Jorge V. Crisci, Warren L. Wagner & Peter C. Hoch* 159

Floral Biology of *Hesperantha* (Iridaceae: Crocoideae): How Minor Shifts in Floral Presentation Change the Pollination System ——— *Peter Goldblatt, Ingrid Nänni, Peter Bernhardt & John C. Manning* 186

Lineage Sorting and Phylogeography in *Lithocarpus formosanus* and *L. dodonaeifolius* (Fagaceae) from Taiwan ——— *Tzen-Yuh Chiang, Kuo-Hsing Hung, Tsai-Wen Hsu & Wen-Luan Wu* 207

Cover illustration. *Trisetum ligulatum* Finot & Zuloaga, drawn by Vladimiro Dudás.

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REVISIÓN TAXONÓMICA DEL GÉNERO *PASPALUM* GRUPO ERIANTHA (POACEAE, PANICOIDEAE, PANICEAE)[1]

Osvaldo Morrone,[2] *Silvia S. Denham*[2] *y Fernando O. Zuloaga*[2]

RESUMEN

El grupo Eriantha de *Paspalum* comprende cinco especies: *P. ammodes*, *P. erianthoides*, *P. erianthum*, *P. guttatum* y *P. paucifolium*, que se distribuyen desde México, en América del Norte, hasta Brasil, Bolivia, Paraguay, Argentina y Uruguay. En el presente tratamiento se definen los caracteres morfológicos del grupo y se incluye una clave para identificar las especies, descripciones, ilustraciones, fotografías y mapas de distribución de las mismas. Se discuten las relaciones de Eriantha con taxones afines de *Paspalum*. Finalmente, se designa un lectótipo para *Paspalum erianthum* Nees var. *strictum* Döll.

ABSTRACT

Eriantha is an American group of *Paspalum* with five species distributed from Mexico in North America to Brazil, Bolivia, Paraguay, Argentina, and Uruguay: *Paspalum ammodes*, *P. erianthoides*, *P. erianthum*, *P. guttatum*, and *P. paucifolium*. Morphological characteristics of the group are defined, and a key to identify the species, descriptions, illustrations, photomicrographs, and distribution maps are provided. Relationships of Eriantha with related taxa of *Paspalum* are discussed. Finally, a lectotype was designated for *Paspalum erianthum* Nees var. *strictum* Döll.

Key words: America, Eriantha, *Paspalum*, Poaceae.

Paspalum L. incluye aproximadamente 320 especies distribuidas en regiones tropicales y subtropicales de América, con cerca de 20 especies en el Viejo Mundo (Clayton & Renvoize, 1986; Zuloaga et al., 2003). El género fue dividido en subgéneros, secciones o grupos informales por diversos autores, principalmente sobre la base de caracteres morfológicos de la inflorescencia, espiguillas y an-

[1] Deseamos expresar nuestro agradecimiento a los curadores de los herbarios consultados, al Sr. Vladimiro Dudás por las excelentes ilustraciones que acompañan esta contribución y a la Lic. Alejandra Garbini por el armado de los mapas. Parte de este estudio se llevó a cabo con fondos de la National Geographic Society, subsidios #5334-94, #6042-97 y #6698-00, que permitieron realizar trabajos de campo y del Consejo Nacional de Investigaciones Científicas y Técnicas, CONICET, Argentina, PIP-02131.

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tecios (Nees, 1829; Doell, 1877; Chase, 1929; Pilger, 1929, 1940; Clayton & Renvoize, 1986; Filgueiras & Davidse, 1994; Morrone et al., 1995, 1996, 2000; Cialdella et al., 1995; Rodríguez, 1999; Denham et al., 2002). Sin embargo no existe un esquema natural de clasificación del género. Zuloaga y Morrone (en prensa) reconocen en *Paspalum* 3 subgéneros, subg. *Anachyris* Chase, subg. *Ceresia* (Pers.) Rchb. y subg. *Paspalum*, e indican que en este último subgénero aún no se encuentran caracteres diferenciales sólidos para establecer categorías infragénericas, por lo que se ha adoptado el concepto de grupos establecido por Chase (1929, inéd).

Pilger (1929) establece la sección *Erianthum* e incluye a *Paspalum erianthum* Nees ex Trin., *P. erianthoides* Lindm. y *P. sordidum* Hack. (= *P. ammodes* Trin.); distingue a la sección principalmente por sus espiguillas velludas.

Swallen (1967) establece diez nuevas especies en el grupo Eriantha: *Paspalum album, P. involutum, P. mollifolium, P. rigens, P. formosulum, P. intosum, P. haughtii, P. sericatum, P. paucifolium* y *P. diamantinum.*

Hasta el presente no se han llevado a cabo estudios del conjunto de las especies de Eriantha, y éstas sólo han sido tratadas parcialmente en estudios florísticos o regionales (Chase, 1929; Burkart, 1969; Rosengurtt et al., 1970; Sendulsky & Burman, 1978, 1980; Judziewicz, 1990; Killeen, 1990; Renvoize, 1984, 1988, 1998; Pohl & Davidse, 1994).

El objetivo del presente trabajo es el estudio de las especies del grupo Eriantha de *Paspalum*, establecer los caracteres diagnósticos a nivel del grupo y de sus especies sobre la base de datos exomorfológicos. El trabajo aporta descripciones, ilustraciones, clave para la identificación de las especies, microfotografías de antecios superiores con microscopía electrónica de barrido, mapas de distribución y ecología de las mismas. Cabe destacar que en la presente revisión no se ha buscado, al agrupar taxones en el grupo Eriantha, establecer categorías taxonómicas a nivel infragenérico.

Historia

Nees (1829) divide a *Paspalum* en seis secciones. Bajo la sección *Lanigeri* trata a *P. guttatum, P. erianthum* y *P. sanguinolentum* junto con *P. ovatum* Nees ex Trin. (= *P. dilatatum* Poir.), *P. polyphyllum* Nees ex Trin. y *P. blepharophorum* Roem. & Schult. (= *P. humboldtianum* Flüggé), *P. conjugatum* Bergius y otras especies consideradas actualmente en *Axonopus* P. Beauv.

Doell (1877) agrupa a las especies de *Paspalum* en cuatro secciones: *Eremachyrion, Opisthion, Emprosthion* y *Cabrerae.* Doell incluye en *Opisthion* a *P. ammodes, P. guttatum* Trin., *P. sanguinolentum* Trin. y *P. erianthum,* entre otras especies afines.

Nash (1912) al estudiar las especies de *Paspalum* de Norte América reconoce informalmente, sin establecer un rango determinado, a Eriantha por incluir plantas con espiguillas pilosas en toda su superfice y cañas simples. Nash incluye una sola especie bajo Eriantha, *P. erianthum.*

Pilger (1929) divide al género *Paspalum* en ocho secciones: *Eupaspalum, Anachyris, Pterolepidium, Erianthum, Cymatochloa, Ceresia, Eriolepidium* y *Moenchia.* Pilger establece la sección *Erianthum* sobre una parte de la sección *Lanigeri* de Nees (1829) representada por *P. erianthum*; cabe destacar que del resto de especies tratadas por Nees (1829) en la sección *Lanigeri, P. obtusifolius* y *P. fissifolius* pertenecen actualmente a *Axonopus, P. eucomum, P. polyphyllum,* y su sinónimo *P. blepharophorum* se ubican en el subgénero *Ceresia, P. ovatum* en el grupo Dilatata y *P. conjugatum* en el grupo Conjugata; finalmente *P. ammodes, P. guttatum* y *P. sanguinolentum* (= *P. erianthum*) son aquí consideradas dentro de Eriantha. Pilger (1929) caracteriza a la sección por los racimos más o menos rectos, raquis delgados, espiguillas sedosas y velludas; incluye en la sección a *P. erianthum, P. erianthoides* y *P. sordidum.*

Chase (1929) considera a *Paspalum sanguinolentum* (= *P. erianthum*) en el subgénero *Ceresia,* aunque indica claramente que Eriantha no pertenece a *Ceresia.* Posteriormente, Chase (inéd.) trata a *Paspalum erianthum, P. rufum* Nees ex Steud., *P. hassleri* Hack. (= *P. rufum*), *P. erianthoides, P. durifolium* Mez y *P. devincenzii* Parodi (= *P. durifolium*) en el grupo Eriantha; mientras que ubica a *P. guttatum* y *P. ammodes* en el subgénero *Ceresia.*

Clayton y Renvoize (1986) reconocen, siguiendo parcialmente el criterio de Pilger (1929, 1940), ocho secciones dentro de *Paspalum*; caracterizan a *Erianthum* por tener espiguillas pilosas, con pelos sedosos y citan, dentro de la sección, a *P. erianthum.*

Materiales y Métodos

El estudio exomorfológico fue realizado sobre la base de especímenes provenientes de los siguientes herbarios: BM, COL, CTES, G, IBGE, ICN, K, LIL, LPB, M, MA, MEXU, MO, P, R, RB, SI, SP, US y W. Dentro del material examinado de cada especie sólo se citaron ejemplares representativos de cada país; una lista completa de los especímenes estu-

diados, ordenados alfabéticamente por coleccionista, se encuentra al final del texto (Apéndice 2).

Las fotomicrografías de antecios superiores se realizaron de acuerdo a los procedimientos descriptos por Soderstrom y Zuloaga (1989). Se empleó un microscopio electrónico de barrido (MEB) Zeiss 940 A, perteneciente al Instituto de Botánica Darwinion, y se operó a 10–20 kV.

Morfología

Forma biológica

El grupo Eriantha de *Paspalum* incluye especies perennes, cespitosas, con rizomas de entrenudos cortos o rizomatosas, con rizomas arqueados en *P. paucifolium*. Las cañas floríferas son erectas y simples, paucinodes en *P. ammodes*, *P. guttatum* y *P. paucifolium* o pueden tener hasta 8 nudos en *P. erianthum*. Las vainas son predominantemente basales en *P. ammodes*, *P. erianthoides*, *P. guttatum* y *P. paucifolium* y basales o distribuidas a lo largo de toda la caña en *P. erianthum*; en *P. ammodes*, *P. erianthum* y *P. guttatum* las vainas son senescentes y persistentes, fibrosas y laciniadas en la base de las plantas; la pilosidad de las vainas varía de glabras a densamente hirsutas o vilosas. Las lígulas son membranáceas, breves, de 0.2–0.8 mm en *P. ammodes*, *P. erianthum* y *P. guttatum*, de 0.5–1.4 mm en *P. paucifolium* y más largas, de 1–2 mm en *P. erianthoides*; en *P. erianthum* y *P. paucifolium* no hay pseudolígula, mientras que en *P. erianthoides* y *P. guttatum* está formada por un arco de pelos de 0.5–2 mm de largo por detrás de la lígula junto a la unión con la lámina; la pseudolígula puede estar presente o ausente en *P. ammodes*; el cuello varía de glabro a piloso. Las láminas son lineares en *P. ammodes* y *P. guttatum*, lineares a linear-lanceoladas en *P. paucifolium* y linear-lanceoladas a lanceoladas en *P. erianthum*, mientras que *P. erianthoides* presenta láminas filiformes y macizas; *P. erianthum* y *P. guttatum* poseen láminas planas a involutas, mientras que en *P. ammodes* son planas a plegadas y planas en *P. paucifolium*; las bases de las láminas son atenuadas o redondeadas a subcordadas, en *P. erianthum* pueden variar de redondeadas a atenuadas formando un pseudopecíolo rígido; el ápice de las láminas va de agudo a subulado; la pilosidad de las láminas es variable hasta en una misma especie, desde glabras a pilosas en ambas caras.

Inflorescencias

Los pedúnculos exertos llevan inflorescencias terminales con racimos adpresos, en *Paspalum erianthoides*, a divergentes y ascendentes en las restantes especies. El número de racimos varía de (1)2 a 11 por inflorescencia, siendo alternos a subopuestos en *P. erianthum*, subconjugados en *P. guttatum* o alternos en las restantes especies; el raquis de los racimos es de 1–12 cm de largo y 0.4–1.8 mm de ancho, triquetro en *P. ammodes* y *P. erianthoides*, o con una de las caras aplanada en *P. erianthum*, *P. paucifolium* y aplanado y cortamente alado en *P. guttatum*; el raquis de los racimos puede terminar en una espiguilla desarrollada u ocasionalmente puede terminar en una prolongación estéril, con espiguillas parcialmente desarrolladas en *P. guttatum*. Las espiguillas son solitarias en *P. guttatum* y *P. ammodes* y en pares en *P. erianthoides*, *P. paucifolium* y *P. erianthum*, donde es frecuente que la espiguilla inferior no se desarrolle por completo y persista como un rudimento en la base de la espiguilla superior.

Espiguillas

Las espiguillas son elipsoides a largamente elipsoides, de 2.4–5(–5.8) mm de largo y 1–2 mm de ancho, plano-convexas, pilosas, con pelos sedosos, blanquecinos, papiloso-pilosas en *Paspalum ammodes*, *P. erianthoides* y *P. paucifolium*. La pilosidad puede ser homogénea, en *P. ammodes*, *P. erianthum*, *P. paucifolium* y *P. guttatum*, o más densa en los márgenes de las brácteas, como en *P. erianthoides*. Los pelos alcanzan hasta 5 mm de largo en *P. guttatum* y entre 1–3.5 mm en el resto de las especies. La gluma inferior se halla ausente, ocasionalmente se la encuentra en espiguillas aisladas en una misma inflorescencia en *P. ammodes*, *P. erianthoides* y *P. erianthum*.

La gluma superior y lemma inferior son subiguales, tan largas como la espiguilla en *Paspalum erianthum* y *P. paucifolium*, y subiguales o la gluma superior es ligeramente más corta, dejando libre el dorso apical del antecio, en *P. ammodes* y *P. erianthum*. En *P. guttatum* la gluma superior es tan larga como la espiguilla y la lemma inferior ligeramente más corta. La gluma superior es 5-nervia, con un nervio central y los restantes marginales y próximos entre sí. La lemma inferior es (3–)5-nervia, cuando 5-nervia, los nervios poseen una distribución similar a la hallada en la gluma superior. La pálea inferior y flor inferior están ausentes en las especies de Eriantha.

Antecio superior

Textura

En las especies del grupo Eriantha de *Paspalum* los antecios son elipsoides, de 2.3–4.5(–5) mm de

largo y 1–1.9(–2) mm de ancho, cartilaginosos y pajizos. La lemma y pálea poseen la cara abaxial finamente papilosa, en *P. ammodes* y *P. paucifolium*, o papilosa en las restantes especies. La superficie del antecio superior está compuesta de células largas rectangulares, más de tres veces más largas que anchas, con las paredes anticlinales longitudinales y transversales onduladas (Fig. 1F). La lemma posee los márgenes enrollados y cubre las 2/3 partes de la superficie de la pálea, encerrando el ápice de la misma (Fig. 1A, D).

Ornamentación del antecio superior

Los antecios presentan papilas distribuidas regularmente sobre la cara abaxial de la lemma y pálea, cuerpos de sílice o micropelos. Las papilas son simples, una por célula, excéntricas, próximas a la pared transversal distal (Fig. 1A–C, F) o verrucosas, las cuales presentan 3–5 verrugas en cada papila, en la pálea de *Paspalum guttatum* (Fig. 1D, E). Los cuerpos de sílice son halteriformes a ligeramente cruciformes (Fig. 1F), exfoliados, dispuestos hacia los márgenes apicales de la lemma y pálea. Micropelos son frecuentes en la zona apical de la pálea junto a los bordes de la lemma (Fig. 1A y D) y en el 1/3 superior de la lemma (Fig. 1B, C). Los micropelos son bicelulares, fusiformes, del tipo "panicoide", con la célula basal de paredes engrosadas y la apical de paredes delgadas, ambas de igual tamaño o la distal dos veces más larga (Fig. 1C). Se observaron ocasionalmente macropelos unicelulares, largos y tiesos hacia el ápice de la lemma y pálea en *P. erianthoides* y *P. paucifolium*.

Distribución Geográfica y Ecología

Las especies de Eriantha habitan desde el sur de México y Centroamérica hasta el noreste de Argentina y norte de Uruguay. La mayor concentración se halla en Sudamérica, particularmente en Bolivia, Paraguay, Argentina, Uruguay y sur de Brasil, donde crecen las cinco especies del grupo. Las especies del grupo Eriantha crecen desde el nivel del mar hasta los 1700 m, en suelos arcillosos, arenosos o rocosos; *P. erianthoides* es frecuente en bañados o cursos de arroyos y ríos. *Paspalum ammodes*, *P. erianthum* y *P. guttatum* crecen frecuentemente en campos abiertos sujetos a fuegos periódicos y es común observar en la base de las plantas restos de vainas persistentes y fibrosas; la persistencia de estas vainas está probablemente relacionada con la protección de las yemas frente a factores ambientales adversos y la adaptación de las plantas a los fuegos frecuentes.

Discusión

De acuerdo con los caracteres morfológicos enunciados, las especies de *Paspalum* del grupo Eriantha se caracterizan por incluir plantas perennes, cespitosas a rizomatosas, con cañas simples, con hojas predominantemente basales, espiguillas elipsoides, solitarias o en pares, pilosas, con pelos sedosos, antecio superior cartilaginoso, pajizo, papiloso, con el ápice de la pálea encerrado por su correspondiente lemma y cariopsis con hilo elíptico.

Se distinguen dentro de Eriantha 2 subgrupos: el primero de ellos está formado por *Paspalum ammodes* y *P. guttatum*, ambas especies con espiguillas solitarias, distribuidas en 2 series. *Paspalum erianthum*, *P. erianthoides* y *P. paucifolium* forman un segundo grupo caracterizado por sus espiguillas en pares (o la inferior abortada) distribuidas en 4 series, en ocasiones en 2 series.

Eriantha se ubica dentro de *Paspalum* junto a otras especies con espiguillas pilosas, como las del subgénero *Ceresia* y los grupos Bertoniana y Fasciculata.

El subgénero *Ceresia* de *Paspalum* incluye 25 especies que habitan desde México hasta la Argentina, Uruguay y sur de Brasil, y se caracteriza por incluir plantas perennes (con unas pocas especies anuales), con láminas rígidas, filiformes a lanceoladas, inflorescencias con 1 a varios racimos, raquis manifiestamente alado, membranáceo a hialino, de 0.8–10 mm de ancho, espiguillas pilosas y antecio superior hialino a membranáceo, con el ápice de la pálea libre (Denham et al., 2002); sus especies crecen usualmente en lugares abiertos y secos como sabanas, campos rupestres y cerrados.

El grupo Bertoniana (Chase, inéd.) incluye 2 especies, *Paspalum bertonii* Hack. y *P. lilloi* Hack., con una distribución restringida al sur de Brasil, este de Paraguay y noreste de Argentina. Ambas especies de este grupo crecen en ambientes húmedos, sobre pendientes y suelos rocosos en márgenes de ríos, cascadas o saltos; las plantas poseen el antecio superior abierto en su extremo, cariopsis con hilo linear y las láminas foliares con costillas adaxiales marcadas.

El grupo Fasciculata de *Paspalum* (Chase, 1929) está integrado por una única especie, *P. fasciculatum* Willd. ex Flüggé, de amplia distribución desde México y América Central hasta Bolivia, Brasil, Paraguay y Argentina. *Paspalum fasciculatum* se halla relacionado a Eriantha por la forma de la espiguilla, largamente elipsoide, con los márgenes papiloso-pestañosos. *Paspalum fasciculatum* se distingue por incluir plantas robustas, rastreras, arrai-

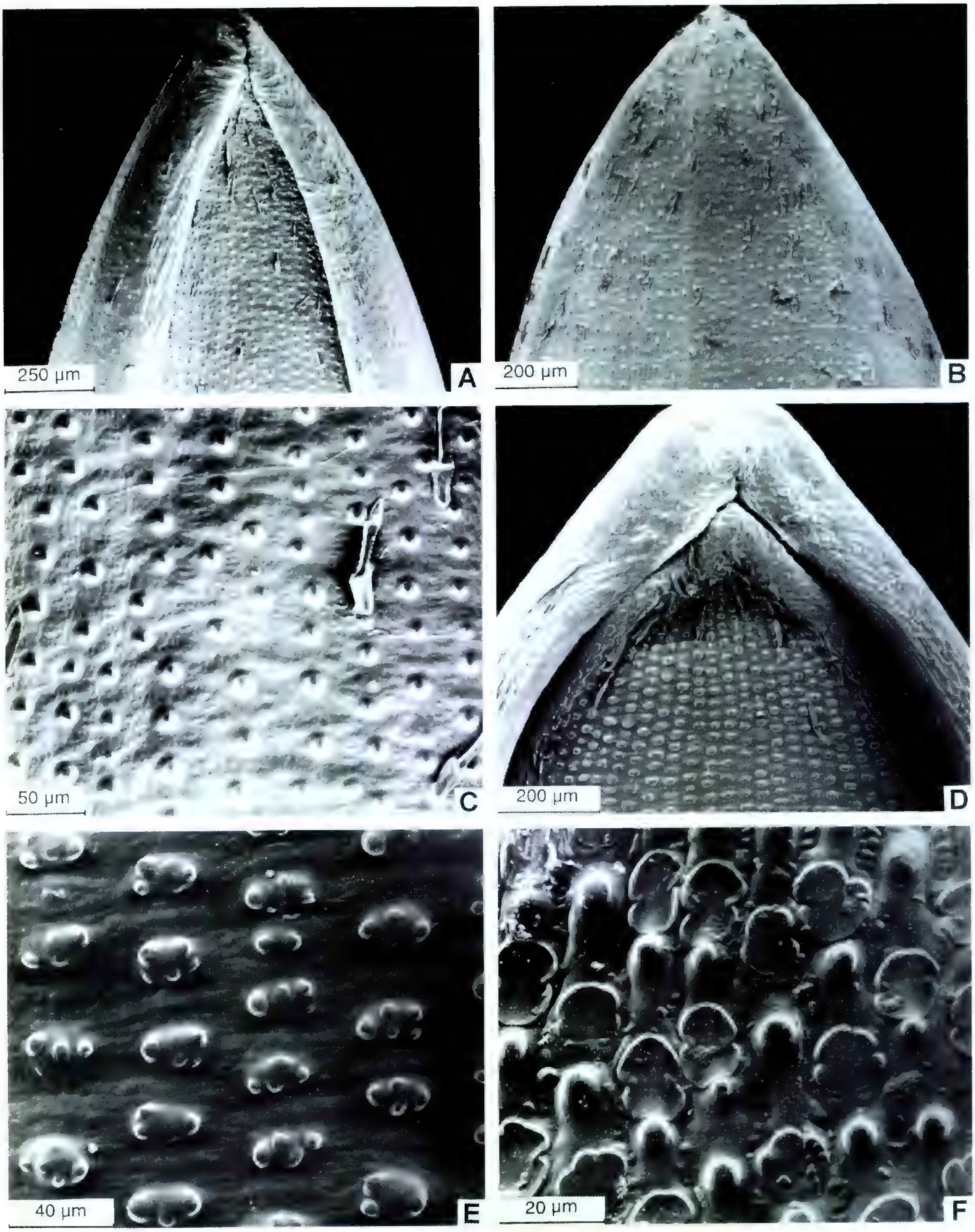


Figura 1. Fotomicrografías de antecios superiores de *Paspalum*. A–C. *Paspalum erianthum* (A y C de *Regnell s.n.*, B de *Killeen 2779*). —A. Antecio superior, visto del lado de la pálea. —B. Antecio superior visto del lado de la lemma. —C. Detalle de la lemma mostrando papilas simples y micropelos bicelulares. D–F. *Paspalum guttatum* (de *Semir et al. 375*). —D. Ápice del antecio superior visto del lado de la pálea. —E. Detalle de la pálea mostrando papilas compuestas. —F. Detalle de la lemma mostrando papilas simples y cuerpos de sílice.

gadas y densamente ramificadas en los nudos inferiores y medios, con inflorescencias flabeladas y por habitar a lo largo de márgenes de ríos y arroyos donde forman embalsados.

Paspalum rufum y *P. durifolium*, especies restringidas al sur de Brasil, Paraguay, Uruguay y Argentina, fueron tratadas por Chase (inéd.) junto con especies de Eriantha básicamente por compartir espiguillas pilosas. No obstante, en el presente tratamiento se considera que ambos taxones no muestran afinidades con las especies aquí tratadas en el grupo Eriantha. Así, *Paspalum rufum* incluye plantas robustas, con hojas planas y cortantes, inflorescencias truncadas y antecios castaño claros, caracteres por los cuales fue reubicada en el grupo Virgata de *Paspalum* por Barreto (1954), criterio seguido más recientemente por Gomes (1995) y Gomes y Monteiro (1996). *Paspalum durifolium*, que comprende plantas robustas, hasta de 2 m de alto, con láminas rígidas, planas a plegadas y cortantes, con inflorescencias piramidales y antecio estramíneo, fue incluida en el grupo Quadrifaria de *Paspalum* por Barreto (1966), Gomes (1995) y Gomes y Monteiro (1996).

Clave para Distinguir Eriantha de Grupos Afines de *Paspalum* en América

1. Raquis foliáceo, aplanado 2
1′. Raquis triquetro 3
2(1). Antecio superior hialino a membranáceo, ocasionalmente cartáceo, el ápice de la pálea libre; inflorescencias no flabeladas; cañas huecas, sin médula esponjosa; plantas de lugares abiertos y secos, en campos rupestres, cerrados, sabanas y laderas rocosas ..... subg. *Ceresia*
2′. Antecio superior cartilaginoso, con ápice de la pálea cubierto por los márgenes de la lemma; inflorescencias flabeladas; cañas con médula esponjosa; plantas de lugares húmedos, a lo largo de márgenes de arroyos y ríos ..... Grupo Fasciculata
3(1). Antecio superior abierto en su ápice; cariopsis con hilo linear; láminas con costillas foliares marcadas ..... Grupo Bertoniana
3′. Antecio superior cerrado en su ápice; cariopsis con hilo elíptico; láminas sin costillas foliares marcadas ..... Grupo Eriantha

Tratamiento Taxonómico

Paspalum grupo **Eriantha**

Plantas perennes, cespitosas a rizomatosas, con *cañas* simples. *Lígulas* membranáceas. *Láminas* lanceoladas a lineares, planas a plegadas o filiformes, de pilosidad variable. *Inflorescencias* terminales, solitarias, formadas por 2–11 racimos, ocasionalmente un racimo solitario, ascendentes o adpresas; raquis de los racimos triquetro o aplanado, terminando en una prolongación estéril o en una espiguilla; espiguillas solitarias o en pares, bi- o tetraseriadas, dispuestas unilateralmente sobre los racimos; pedicelos breves. *Espiguillas* elipsoides a largamente elipsoides, plano-convexas, pilosas. *Gluma inferior* ausente. *Gluma superior* 5-nervia. *Lemma inferior* glumiforme, (3–)5-nervia. *Antecio superior* elipsoide, cartilaginoso, pajizo, cerrado en su ápice, papiloso, con micropelos bicelulares hacia el ápice de la lemma y la pálea. *Cariopsis* con hilo subbasal, elíptico; embrión ⅓–½ del largo de la cariopsis.

Grupo integrado por 5 especies americanas, distribuidas desde México hasta el noreste de Argentina, sur de Brasil, Paraguay y Uruguay (se presenta una lista de estas especies en el Apéndice 1; un índice de nombres científicos se encuentra en el Apéndice 3).

Clave para Distinguir las Especies del Grupo Eriantha

1. Espiguillas solitarias 2
1′. Espiguillas en pares, en ocasiones la inferior reducida o abortada (pero los pedicelos siempre en pares) 3
2(1). Racimos 2, raro 1 ó 3, subconjugados; raquis de los racimos cortamente alado, de 1–1.8 mm de ancho; lígula de 0.2 mm de largo; espiguillas elipsoides de 4–5 mm de largo, 1.5–2 mm de ancho, densamente vilosas, con pelos de 4–5 mm de largo ..... 4. *P. guttatum*
2′. Racimos (1–)2–6, alternos; raquis de los racimos triquetro, de 0.4–0.6 mm de ancho; lígula de 0.4–0.6 mm de largo; espiguillas largamente elipsoides, de 2.4–3.8 mm de largo, 1–1.2 mm de ancho, pilosas, con pelos de 1–2 mm de largo ..... 1. *P. ammodes*
3(1). Láminas filiformes, macizas; inflorescencias subespiciformes, de 1–1.5 cm de ancho; raquis de los racimos triquetro, de 0.4–0.5 mm de ancho ..... 2. *P. erianthoides*
3′. Láminas lineares o linear-lanceoladas, planas a involutas; inflorescencias no subespiciformes, de 1–6(–10) cm de ancho; raquis de los racimos aplanado, de 0.5–1.3(–1.5) mm de ancho 4
4(3). Plantas con rizomas horizontales, viajeros, arqueados; vainas predominantemente basales, rodeadas de catáfilos en la base; láminas predominantemente basales, las superiores reducidas; racimos 2–4 ..... 5. *P. paucifolium*
4′. Plantas de rizomas de entrenudos cortos, densamente cespitosas; vainas basales y a lo largo de las cañas floríferas, las basales persistentes, fibrosas, laciniadas; láminas basales o distribuidas a lo largo de las cañas; racimos 2–10 ..... 3. *P. erianthum*

1. Paspalum ammodes Trin., Gram. Panic.: 120. 1826. TIPO: Brasil. Minas Gerais: "in arenosis pr. Tejuco", *G. H. von Langsdorff s.n.* (holótipo, LE-TRIN-0415.01!, fotos, K!, SI!; isótipo, US-

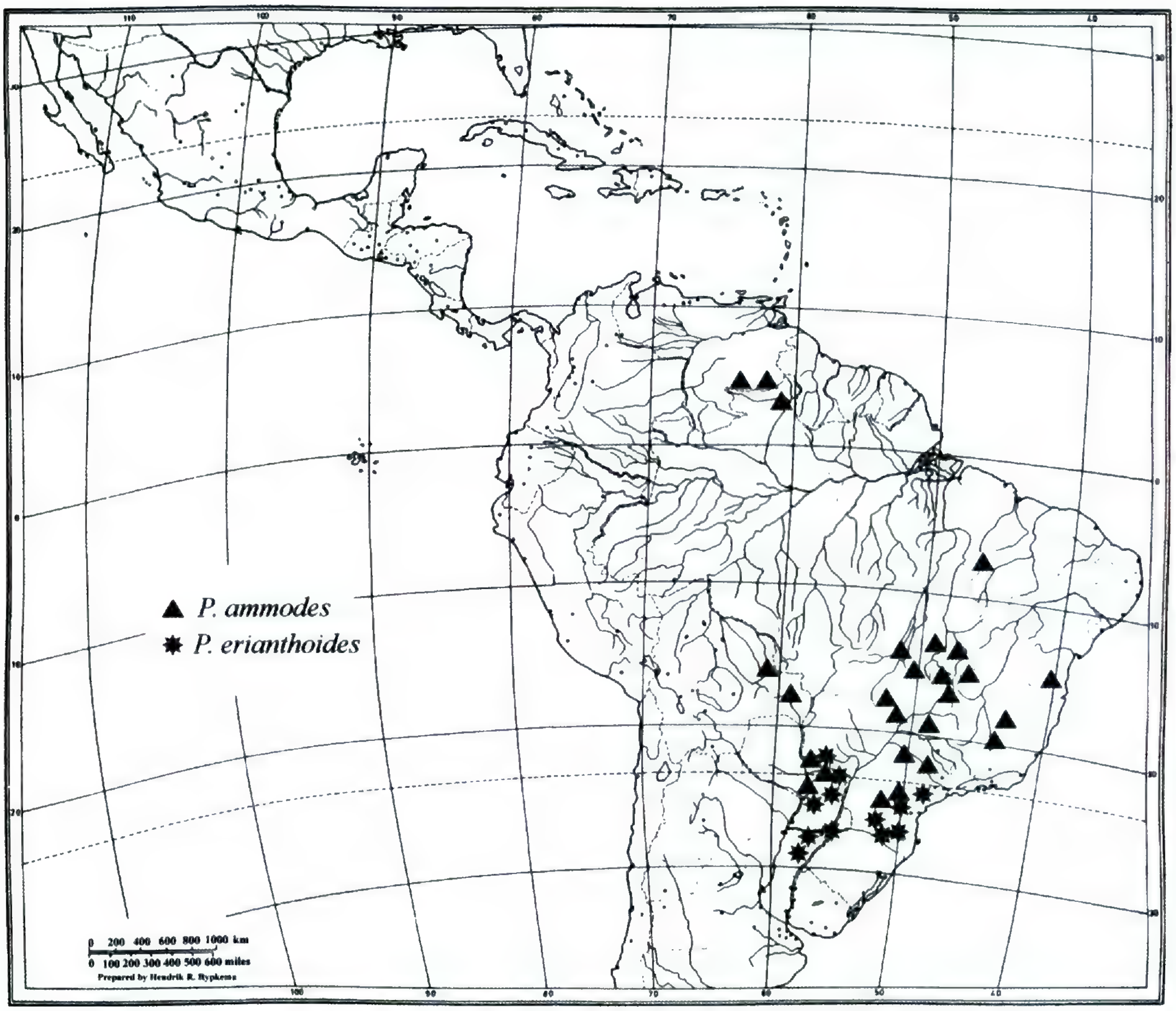


Figura 2. Distribución de *Paspalum ammodes* y *P. erianthoides*.

2941973!; probable isótipo, *L. Riedel 969*, B!). Figura 3.

Paspalum sordidum Hack., Oesterr. Bot. Z. 51: 197. 1901. TIPO: Brasil. Goiás: Rio Corto, 21 Nov. 1896, *A. F. M. Glaziou 22472* (lectótipo, designado por Zuloaga & Morrone (2003: 515), W!; isótipos, K!, P!, US-555444!, US-2856003!, foto, SI!).

Paspalum diamantinum Swallen, Phytologia 14: 368. 1967. TIPO: Brasil. Minas Gerais: Diamantina, Serra de San Antonio, 1200–1300 m, 27–30 dic. 1929, *A. Chase 10401* (holótipo, US no visto; isótipo, MO-1002695!).

Paspalum canum Sohns, Mem. New York Bot. Gard. 9: 256, f. 6. 1957. TIPO: Brasil. Roraima: Rio Branco, frequent along stream course E slope of Serra Marico, 1100 m, 16–18 dic. 1954, *B. Maguire & C. Maguire 40349* (holótipo, US-2182187!; isótipos, K!, NY!, P!).

Plantas perennes, con rizomas breves, rígidos; *cañas* de 20–70 cm de largo, 0.2 cm de diámetro, erectas, paucinodes; entrenudos 2–3, de 7–25 cm de largo, cilíndricos a comprimidos, huecos, glabros a esparcidamente pilosos; nudos densamente barbados a glabros. *Vainas* más cortas que los entrenudos, predominantemente basales, comprimidas, aquilladas, las viejas persistentes, laciniadas, fibrosas, glabras a densamente hirsutas, con los márgenes glabros a ciliados; *lígulas* breves, de 0.4–0.6 mm de largo, glabras; pseudolígula ausente o presente, cuando presente fomada por largos pelos blanquecinos hasta de 2 mm de largo; cuello glabro a piloso; *láminas* lineares, de 3–25 cm de largo, 0.2–0.3 cm de ancho, las superiores reducidas, falcadas, plegadas o planas, predominantemente basales, glabras a esparcidamente hirsutas, de base atenuada, continuándose imperceptiblemente con la vaina, el ápice agudo a subulado, los márgenes escabrosos, glabros, los basales pestañosos. *Pedúnculos* exertos, hasta de 25 cm de largo, cilíndricos, glabros; *inflorescencias* terminales, de 2.4–10 cm de largo, 1–4 cm de ancho; eje principal de 1–4 cm de largo, anguloso, glabro, liso a escabroso; pulvínulos largamente pilosos, con un mechón de pelos blanquecinos; racimos 2–6, raro un racimo solita-

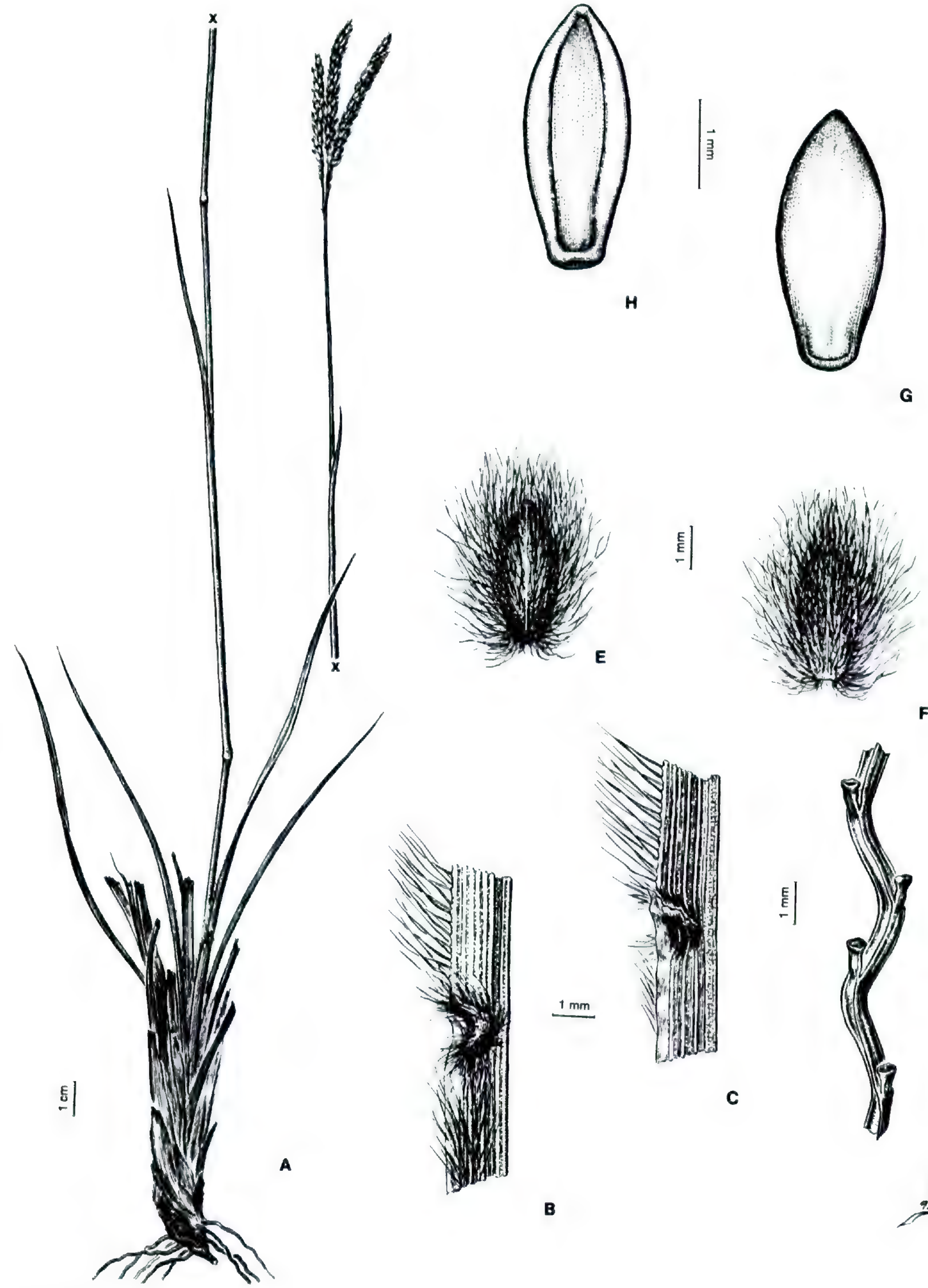


Figura 3. *Paspalum ammodes* (de *Rojas 6316*). —A. Hábito. —B. Detalle de la región ligular, cara externa. —C. Detalle de la región ligular, cara interna. —D. Detalle de una porción de racimo. —E. Espiguilla vista del lado de la gluma superior. —F. Espiguilla vista del lado del la lemma inferior. —G. Antecio superior visto del lado de la lemma. —H. Antecio superior visto del lado de la pálea.

rio, ascendentes, alternos, divergentes del eje principal, terminando en una espiguilla desarrollada, en ocasiones vestigial; raquis de los racimos de 2–8 cm de largo, 0.4–0.6 mm de ancho, triquetro, sinuoso, verdoso o con tintes violáceos, con la cara adaxial glabra, las restantes caras hispídulas, los márgenes escabriúsculos; pedicelos solitarios, breves, hasta de 1 mm de largo, glabros; espiguillas solitarias, no imbricadas, dispuestas en 2 series. *Espiguillas* largamente elipsoides, de 2.4–3.8 mm de largo, 1–1.2 mm de ancho, de ápice agudo a obtuso, plano-convexas, pilosas, grisáceo-verdosas o con tintes violáceos o rojizos; gluma superior y lemma inferior subiguales o la gluma superior ligeramente menor, membranáceas, homogéneamente papiloso-pilosas, con pelos sedosos de 1–2 mm de largo; *gluma inferior* ausente, ocasionalmente presente, escamiforme, hasta de 1 mm de largo, enervia; *gluma superior* tan larga como la espiguilla o ligeramente menor, dejando libre el dorso apical del antecio superior, 5-nervia, con un nervio central, los restantes submarginales; *lemma inferior* glumiforme, tan larga como la espiguilla, 5-nervia; *antecio superior* elipsoide, de 2.3–3.5 mm de largo, 1–1.2 mm de ancho, más corto que la gluma superior y lemma inferior o alcanzando el largo de las mismas, cartilaginoso, pajizo, glabro, finamente papiloso, con papilas simples; lemma con papilas regularmente distribuidas y micropelos bicelulares hacia el ápice, 5-nervia, con los márgenes enrollados sobre la pálea; pálea de textura similar a la lemma con papilas regularmente distribuidas y micropelos bicelulares hacia los márgenes apicales y el ápice; lodículas 2, de 0.4–0.5 mm de largo; estambres 3, anteras de 1.8–2 mm de largo. *Cariopsis* elipsoide, de 2.7 mm de largo, 1.1 mm de ancho; hilo elíptico, un poco menos de la mitad de la cariopsis; embrión 1/3 del largo de la cariopsis.

Distribución geográfica y ecología. Crece desde Venezuela, Guyana (citado por Judziewicz, 1990) y Brasil hasta Bolivia y Paraguay (Fig. 2). Habita en campos sobre suelos arenosos o rocosos, o en suelos húmedos, en zonas de fuegos periódicos, formando pequeñas matas entre los 0–1600 m s.m.

Nombre vulgar. "Capim-touceira" (Brasil, Smith et al., 1982).

Paspalum ammodes es afín a *P. guttatum*, distinguiéndose esta última por sus inflorescencias formadas por 2 racimos subconjugados, raro 1 o 3, cortamente alados (de 1–1.8 mm de ancho), espiguillas imbricadas de 4–5 mm de largo, densamente vilosas, con gluma superior 0.8–1 mm más larga que el antecio superior, con los nervios laterales fuertemente marcados y lígula de 0.2 mm de largo.

La gluma inferior se halla comúnmente ausente en las espiguillas de *Paspalum ammodes*; ocasionalmente fue observada en espiguillas aisladas de una misma inflorescencia en los ejemplares *Rojas 6316*, *Chase 10401*, *Brito 150* e *Irwin & Soderstrom 7395*, en los que puede ser rudimentaria, escamiforme a lanceolada alcanzando aproximadamente ⅓ del largo de la espiguilla.

Paspalum ammodes se asemeja a *P. erianthum* por la morfología de la espiguilla, apartándose esta última por tener espiguillas en pares, de mayor tamaño [de 3–5(–5.8) mm de largo] y láminas lanceoladas a linear-lanceoladas.

El ejemplar *Riedel 969* coleccionado en Brasil, sin indicar localidad precisa, examinado en el Herbario del Museo Botánico Berlin-Dahlem (B) probablemente corresponda a un isótipo de *P. ammodes* [para una discusión más detallada sobre las colecciones realizadas por G. H. von Langsdorff y L. Riedel y descriptas por C. B. Trinius véase Renvoize (1978)].

Hackel (1901) al describir *Paspalum sordidum* cita dos síntipos coleccionados en Goiás, Brasil, *Glaziou 22477* y *22472*, de los cuales este último es selecionado como lectótipo por coincidir con el protólogo de la especie.

Filgueiras (1993) considera a *Paspalum diamantinum* Swallen un taxón dudoso y menciona que podría ser conespecífico con *P. erianthoides*. El análisis de la descripción original realizada por Swallen (1967), del material tipo y de un parátipo citado por este autor (*Chase 10347*, BM, K, US, W), permitió verificar que esta especie es en realidad un sinónimo de *P. ammodes*.

Material adicional examinado. BOLIVIA. **Santa Cruz:** Chiquitos, Serranía de Santiago, 3 km N of Santiago de Chiquitos, *Killeen 2786* (MO, US). BRASIL. **Bahia:** 5 km de Rio de Contas, *Zuloaga et al. 4832* (MO, SI). **Distrito Federal:** 10 km W of Taguatinga, on road to Brasilândia, *Irwin et al. 10635* (US). **Goiás:** ca. 50 km S of Caiaponia on road to Jataí, *Irwin & Soderstrom 7395* (G, US). **Maranhão:** Balsas, *Oliveira & da Silva 374* (SI). **Minas Gerais:** Diamantina, Serra de San Antonio, *Chase 10347* (BM, K, US, W). **Paraná:** Jaguariaiva, *Dusén 16025* (BM, G, MA, P, SI). **São Paulo:** San José dos Campos, *Morello s.n.* (SI). PARAGUAY. **Amambay:** Cabecera Aquidabán, pendiente S Amambay, *Rojas 6316* (US). **Caaguazú:** campos al E de Caaguazú, *Balansa 71* (BM, G, K, P, US). VENEZUELA. **Bolívar:** Dist. Roscio, cuenca del Río Arabopó, aprox. 5 km de la frontera con el Brasil, *Huber & Alarcón 10505* (MO).

2. Paspalum erianthoides Lindm., Kongl. Svenska Vetensk. Handl. 34: 6, tab. 10B. 1900. TIPO: Paraguay. Guairá: Villa Rica, 10 Oct. 1874, *B. Balansa 72* (holótipo, S no visto; isó-

tipos, BM!, G!, K!, LE!, P!, foto, SI!, US-2854688!). Figura 4.

Paspalum dusenii Hack., Ark. Bot. 9: 5. 1910. TIPO: Brasil. Paraná: Curitiba, in paludosis, 29 Nov. 1903, *P. K. H. Dusén 2331* (holótipo, W!; isótipos, BM!, MO-934883!, US-2854673!).

Plantas perennes, formando densas matas, con rizomas robustos, de entrenudos cortos, verticales, cubiertos por catáfilos seríceos, con pelos sedosos, pardo-rojizos; *cañas* de 80–150 cm de alto, 0.2–0.4 cm de diámetro, erectas, paucinodes, glabras, entrenudos de 15–45 cm de largo, huecos; nudos comprimidos, castaños a negruzcos, glabros. *Vainas* de 15–25 cm de largo, predominantemente basales, aquilladas, las basales seríceas hacia la porción distal, con pelos largos, adpresos, pardo-rojizos hacia la región ligular, vainas apicales glabras a pilosas, con pelos blanquecinos hacia la región ligular, el resto de la superficie glabra, los márgenes cortamente ciliados a glabros; *lígulas* de 1–2 mm de largo, glabras, castañas; pseudolígula presente, con largos pelos por detrás en la base de la lámina, pardo-rojizos; cuello densamente glabro a piloso, con pelos pardo-rojizos; *láminas* filiformes, de 30–60 cm de largo, 1–2 mm de ancho, predominantemente basales, reducidas hacia el ápice de las cañas, rígidas, macizas, glabras, de base atenuada y ápice pungente, los márgenes glabros, pestañosos hacia la base. *Pedúnculos* largamente exertos, hasta de 50 cm de largo, cilíndricos, glabros; *inflorescencias* terminales subespiciformes, de 6–25 cm de largo, 1–1.5 cm de ancho; eje principal de 5–19 cm de largo, aplanado, glabro; pulvínulos glabros o con unos pocos pelitos tiesos; racimos 3–11, adpresos al eje principal, alternos, los superiores próximos, terminando en una espiguilla desarrollada; raquis de los racimos de 1–8 cm de largo, 0.4–0.5 mm de ancho, triquetro, flexuoso, glabro, liso; pedicelos desiguales, hasta de 2 mm de largo, escabriúsculos; espiguillas en pares, imbricadas en 4 series, densamente dispuestas a lo largo del raquis de los racimos. *Espiguillas* largamente elipsoides, de 4–5 mm de largo, 1.5–2 mm de ancho, de ápice agudo, plano-convexas, largamente pilosas en los márgenes, verde pálidas y con tintes cobrizos; gluma superior y lemma inferior subiguales, membranáceas, con los márgenes papiloso-pestañosos, con pelos blanquecinos, sedosos, hasta de 2.5 mm de largo, el resto de la superficie glabra a cortamente pilosa en la porción central; *gluma inferior* ausente, ocasionalmente presente hasta 1/2 del largo de la espiguilla, pilosa; *gluma superior* tan larga como la espiguilla, 5-nervia, con un nervio central y los restantes próximos a los márgenes; *lemma inferior* gluminforme, tan larga como la espiguilla, 5-nervia; *antecio superior* elipsoide, de 3.9–4.5 mm de largo, 1.6–1.9 mm de ancho, 0.5 mm más corto que la gluma superior y lemma inferior o alcanzando el mismo largo, cartilaginoso, pajizo, papiloso, glabro o con macropelos largos, tiesos hacia el ápice de la lemma; lemma con papilas simples, distribuidas regularmente y micropelos bicelulares, 5-nervia, los márgenes enrollados sobre la pálea; pálea de textura similar que la lemma, con papilas simples distribuidas regularmente y con micropelos bicelulares hacia los márgenes apicales; lodículas 2, ca. 0.4 mm de largo; estambres 3, anteras de 2.4–3 mm de largo. *Cariopsis* no vista.

Distribución geográfica y ecología. Habita en en el sur de Brasil (Paraná y Santa Catarina), Paraguay Oriental (Amambay, Central y Guairá) y el noreste de Argentina (Corrientes y Misiones) (Fig. 2); crece frecuentemente en bañados, en márgenes de cursos de arroyos y ríos desde el nivel del mar hasta los 1000 m s.m.

Nombre vulgar. "Maceza-do-Banhado" (Brasil, Smith et al., 1982).

Paspalum erianthoides es morfológicamente similar a *P. erianthum* y *P. paucifolium*, especies con las que comparte espiguillas largamente elipsoides y de similar tamaño, con gluma superior y lemma inferior largamente pilosas hacia los márgenes. *Paspalum erianthoides* se distingue por sus inflorescencias subespiciformes y hojas filiformes, macizas (vs. inflorescencias abiertas y hojas lineares a lanceoladas en *P. erianthum* y *P. paucifolium*).

Material adicional examinado. ARGENTINA. **Corrientes:** Dep. Santo Tomé, Garruchos, *Burkart 19732* (SI); Dpto. Ituzaingó, Ruta Nac. 12, 5 km antes del Arroyo Itaembé, *Zuloaga et al. 3234* (MO, SI). **Misiones:** Dep. Apóstoles, Esc. Agrotécnica, *Cabrera 28759* (SI). BRASIL. **Paraná:** Mun. Teixeira Soares, Río das Almas, *Hatschbach 15356* (K, US); Capão da Imbuia, *Dombrowski 2105* (K). **Santa Catarina:** Mun. Abelardo Luz, 8–12 km N of Abelardo Luz, *Smith & Klein 13323* (K, P, US); Mun. Curitibanos, 5 km N of Curitibanos, *Smith & Klein 15482* (K, P, US); Mun. Campo Ere, 6 km W of Campo Ere, *Smith & Klein 13680* (K, MO, US). PARAGUAY. **Amambay:** in altaplanitie Sierra de Amambay, *Hassler 11665* (G, US); in regione calcare cursus superioris fluminis Apa, *Hassler 11941* (G); Nat. Park Cerro Corá, swamp on black humid soil alongo Aceite-i creek, *Zardini & Báez 52369* (MO). **Central:** Prope Sapucay, *Hassler 12906* (BM, G, US).

3. **Paspalum erianthum** Nees ex Trin., Gram. Panic.: 121. 1826. TIPO: Brasil. Minas Gerais: Lagoa Santa, Oct., *G. H. von Langsdorff s.n.* (holótipo, LE-TRIN- 0450.03!; isótipos, LE!, US-2854690!; probable isótipo, *L. Riedel 724*, P!, foto, SI!). Figura 5.

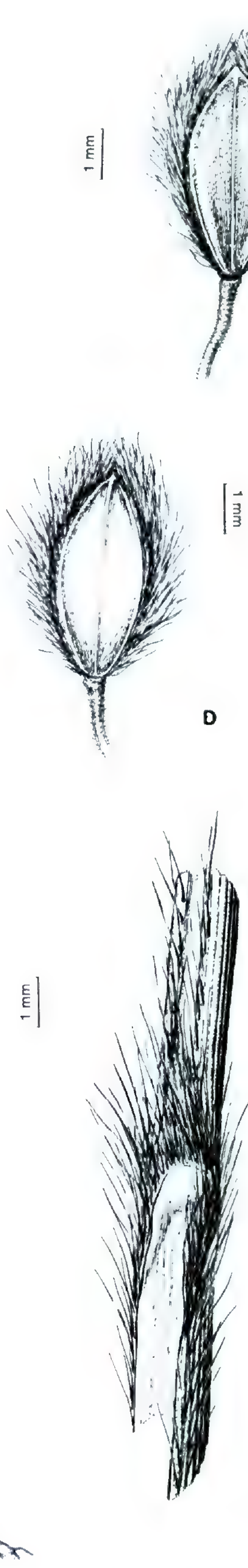


Figura 4. *Paspalum erianthoides* (de *Hassler 10673*). —A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción de racimo. —D. Espiguilla vista del lado de la gluma superior. —E. Espiguilla vista del lado de la lemma inferior. —F. Antecio superior visto del lado de la lemma. —G. Antecio superior visto del lado de la pálea.

Figura 5. *Paspalum erianthum.*—A. Hábito. —B. Detalle de la región ligular. —C. Espiguilla vista del lado de la gluma superior. —D. Espiguilla vista del lado de la lemma inferior. —E. Antecio superior visto del lado de la lemma superior. —F. Antecio superior visto del lado de la pálea. —G. Cariopsis, vista escutelar. —H. Cariopsis, vista hilar. (A, de *Hassler 11924*; B–H, de *Hassler 10765a.*)

Paspalum sanguinolentum Trin., Gram. Panic.: 116. 1826. TIPO: Brasil. Minas Gerais: "in graminosis subhumidis S. da Lapa", dic. 1824, *G. H. von Langsdorff s.n.* (holótipo, LE-TRIN-0526.02!; isótipos, B!, LE!, fragmento US-2855985! ex LE, probable isótipo, *L. Riedel 189*, K!).

Paspalum erianthum Nees, Fl. Bras. Enum. Pl. 2: 38. 1829, hom. illeg. TIPO: Brasil. Sin localidad, *F. Sellow 1230* (lectótipo, designado por Zuloaga & Morrone (2003: 466), B!; isótipos, K!, foto, SI!, P!, US-952193!, US-557565!, US-1441526!).

Paspalum erianthum Nees var. *strictum* Döll, in Martius, Fl. Bras. 2(2): 70. 1877. TIPO: Brasil. Minas Gerais: Caldas, *A. F. Regnell III-1336* (lectótipo, aquí designado, W!; isótipos, G!, US-2854689!, US-1649820!).

Paspalum album Swallen, Phytologia 14: 367. 1967. TIPO: Brasil. Minas Gerais: Diamantina, Serra de San Antonio, 1200–1300 m, 27–30 dic. 1929, *A. Chase 10397* (holótipo, US-1500420!, foto, SI!; isótipo, SI!).

Paspalum involutum Swallen, Phytologia 14: 368. 1967. TIPO: Brasil. Minas Gerais: Diamantina, Serra de San Antonio, 1200–1300 m, 27–30 dic. 1929, *A. Chase 10400* (holótipo, US-1500757!, foto, SI!).

Paspalum mollifolium Swallen, Phytologia 14: 369. 1967. TIPO: Brasil. Minas Gerais: Serra da Bocaina, near Faria, 1000–1200 m, 6 jan. 1930, *A. Chase 10522* (holótipo, US-1500690!, foto, SI!; isótipo, US-2305237!).

Paspalum rigens Swallen, Phytologia 14: 369. 1967. TIPO: Brasil. Minas Gerais: 5–10 km W of Diamantina, Serra de San Antonio, 1300–1500 m, 27–30 dic. 1929, *A. Chase 10442* (holótipo, US-1500399!, foto, SI!).

Paspalum intosum Swallen, Phytologia 14: 370. 1967. TIPO: Brasil. Minas Gerais: Hargreaves, 1350–1400 m, 21–22 dic. 1929, *A. Chase 10268 1/2* (holótipo, US-1501433!).

Paspalum haughtii Swallen, Phytologia 14: 370. 1967. TIPO: Colombia. Vichada: Los Llanos, ca. 60 km S 60º E of Orocué, ca. 150 m, 19 abr. 1939, *O. Haught 2771* (holótipo, US-1706822!, foto, SI!; isótipo, COL-2464!).

Paspalum sericatum Swallen, Phytologia 14: 371. 1967. TIPO: Brasil. Minas Gerais: Serra do Cipó, 110 km NE of Belo Horizonte, Chapeo [Chapéu] de Sol, 1000–1100 m, 28 mar.–1 abr. 1925, *A. Chase 9213* (holótipo, US-1255284!, foto, SI!; isótipo, MO-930663!).

Paspalum formosulum Swallen, Phytologia 14: 372. 1967. TIPO: Brasil. Minas Gerais: Hargreaves, 1350–1400 m, 21–22 dic. 1929, *A. Chase 10268* (holótipo, US-1501432!, foto, SI!; isótipo, US-1501401!, foto, SI!).

Paspalum trichoides R. Guzmán, Phytologia 51: 468. 1982. TIPO: México. Oaxaca: in vicinity of San Juan Guichicovi, 1450–1500 ft., 21–24 June 1985, *E. W. Nelson 2734a [error por 2735a]* (holótipo, US-95220!).

Plantas perennes, con rizomas horizontales de entrenudos cortos, rígidos, cubiertos por catáfilos densamente pilosos, con pelos amarillos, adpresos; *cañas* de (20–)50–130 cm de alto, 0.2–0.4 cm de diámetro, erectas, de base engrosada, subbulbosa; entrenudos 2–8, de 6–35 cm de largo, huecos, comprimidos, glabros, estriados; nudos glabros a densamente pilosos, con pelos patentes, blanquecinos. *Vainas* de 7–25 cm de largo, aquilladas, glabras a vilosas o híspidas, con pelos blanquecinos, adpresos, los márgenes pestañosos; *lígulas* breves, de 0.4–0.8 mm de largo, castañas, pseudolígula ausente; cuello glabro a piloso; *láminas* lanceoladas a linear-lanceoladas, de 4–30 cm de largo, (0.1–) 0.3–1.6(–2) cm de ancho, planas o involutas, ascendentes, distribuidas a lo largo de las cañas o predominantemente basales, verdosas o con tintes purpúreos, glabras a densamente vilosas o híspidas en ambas caras, con pelos cortos, a cortamente pilosas en la cara adaxial y glabras en la abaxial, de base redondeada a angostada en las láminas inferiores, formando un pseudopecíolo rígido, el ápice agudo, los márgenes escabriúsculos a pestañosos hacia la base o en toda su extensión. *Pedúnculos* largamente exertos, hasta de 50 cm de largo, cilíndricos, glabros; *inflorescencias* terminales estrechas, de 5–20 cm de largo, 1–6(–10) cm de ancho; eje principal de 2.5–13 cm de largo, anguloso, glabro a esparcidamente piloso, escabriúsculo; pulvínulos largamente pilosos, con pelos blanquecinos hasta de 7 mm de largo; racimos 2–10, ligeramente divergentes del eje principal a patentes, alternos a subopuestos, más o menos distantes, separados a 1–5 cm, los basales de 4–12 cm de largo, los superiores de menor tamaño, terminando en una espiguilla desarrollada; raquis de los racimos de 0.5–1.2(1.5) mm de ancho, aplanado, verde a purpúreo, glabro o con unos pocos pelitos aislados a hispídulo, con los márgenes escabriúsculos; pedicelos desiguales, hasta de 2 mm de largo, escabriúsculos, con pelos dispersos; espiguillas en pares, en ocasiones la inferior abortada, imbricadas, en 4 series, densamente dispuestas sobre el raquis de los racimos. *Espiguillas* elipsoides a largamente elipsoides, de 3–5(–5.8) mm de largo, 1–2 mm de ancho, sin los pelos, de ápice agudo, plano-convexas, pilosas, con pelos blanco-plateados, la superficie pajiza o con tintes purpúreos a purpúreas; gluma superior y lemma inferior subiguales o la gluma superior ligeramente más corta, membranáceas, con los márgenes y la base densamente pilosas, con pelos ascendentes o la gluma superior densamente vilosa en toda su superficie, con pelos blanquecinos, sedosos, plateados, flexuosos o rectos, hasta de 3.5 mm de largo, la lemma inferior cortamente pubescente a glabra en su parte media; *gluma inferior* ausente, en ocasiones presente, cuando presente hasta 3/4 del largo de la espiguilla, enervia o 1-nervia; *gluma superior* tan larga como la espiguilla, en ocasiones ligeramente más corta y dejando al descubierto el ápice del antecio superior, 5-nervia, con un nervio central, los restantes submarginales;

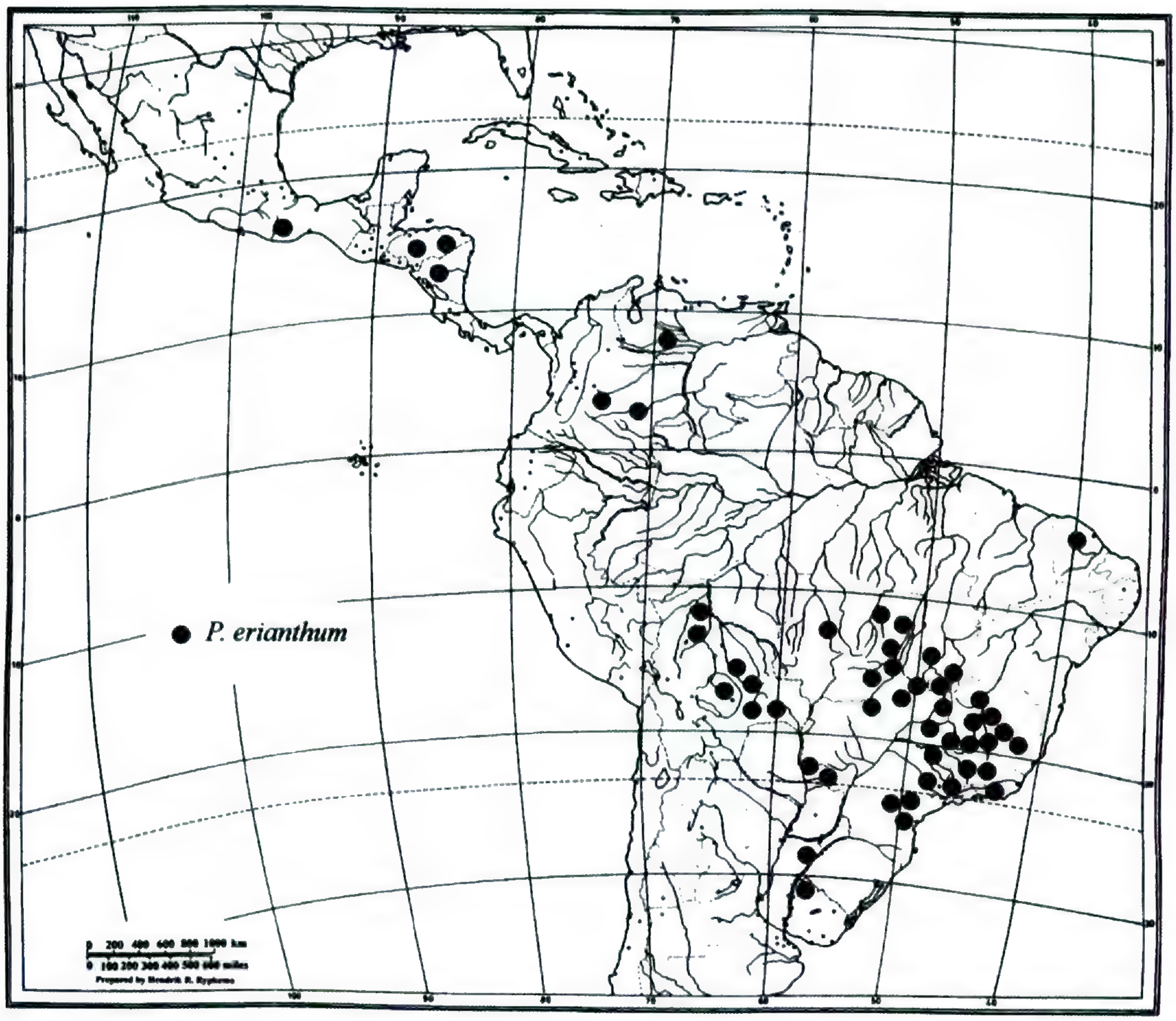


Figura 6. Distribución de *Paspalum erianthum.*

lemma inferior glumiforme, tan larga como la espiguilla, (3–)5-nervia; *antecio superior* elipsoide, de 2.8–4(–5) mm de largo, 1–1.5(–2) mm de ancho, 0.4–0.8 mm más corto que la lemma inferior o alcanzando en largo a la misma, cartilaginoso, pajizo, papiloso, glabro; lemma con papilas simples, regularmente distribuidas y micropelos bicelulares en su dorso, los márgenes enrollados sobre la pálea, 5-nervia; pálea de textura similar a la lemma, con papilas simples distribuidas regularmente y con micropelos bicelulares hacia los márgenes apicales; lodículas 2, ca. 0.4 mm de largo; anteras 3, estambres de 2.1–2.8 mm de largo. *Cariopsis* elipsoide, de 2.4 mm de largo, 1.1 mm de ancho; hilo elíptico, 1/3 del largo de la cariopsis; embrión 1/2 del largo de la cariopsis.

Distribución geográfica y ecología. Habita desde el sur de México y Mesoamérica, en Honduras y Nicaragua, hasta Sudamérica, en Colombia, Venezuela, donde es ocasional, y en Bolivia, Brasil, Paraguay, noreste de Argentina y norte de Uruguay (habiendo sido citada para el Dpto. Artigas de este último país por Rosengurtt et al., 1970 y Smith et al., 1982) (Fig. 6); crece en cerrados y en campos rupestres, en suelos lateríticos o arenosos.

Nombre vulgar. "Macega-do-banhado" (Brasil, Smith et al., 1982).

Número cromosómico. $2n = 80$ (Gould & Soderstrom, 1967; Norrmann et al., 1994).

Paspalum erianthum es afín a *P. erianthoides* (véanse los comentarios bajo esta última especie), distinguiéndose esta última por tener hojas filiformes, macizas e inflorescencias subespiciformes, hasta de 1.5 cm de ancho.

En los ejemplares *Glaziou 22589, Irwin et al. 9603* y *Harley 10495* se observó la presencia de gluma inferior en espiguillas aisladas en una misma inflorescencia; la misma puede ser rudimentaria, escamiforme a linear-lanceolada, alcanzando en ocasiones hasta 3/4 del largo de la espiguilla.

Esta especie es marcadamente variable en la presencia de indumento en las hojas. Así, se ob-

servaron en el espécimen *Irwin et al. 9603* láminas y vainas densamente vilosas; otros, como *Irwin et al. 9197* y *Killeen 1369*, presentan vainas glabras y láminas cortamente pilosas, mientras que en *Irwin & Soderstrom 6807* se hallan vainas glabras e hirsutas en una misma planta. También es manifiesta la variación en el tamaño de la espiguilla: el isótipo *Langsdorff s.n*, depositado en US, posee espiguillas de 3.5 mm de largo, algo menores a lo usualmente presente en esta especie. Asimismo, se han hallado ejemplares con espiguillas algo menores en los especímenes *Irwin et al. 7948* y *Filgueiras & Zuloaga 2207*, los que tienen espiguillas de 3.4 mm de largo; por el contrario, el ejemplar *Hatschbach 35422* presenta espiguillas de 5 a 5.8 mm de largo. Por otra parte, la disposición de las hojas es marcadamente variable, hallándose especímenes con hojas distribuidas a lo largo de las cañas y otros con las láminas predominantemente basales. Es muy probable que estas diferencias se deban a que han sido coleccionados con posterioridad a la actividad de fuegos, ya que en ellos se pueden observar sus bases quemadas. Esto podría tener un efecto diferencial en el crecimiento de las plantas, mostrando éstas un hábito diferente.

En el Herbario del Museo Nacional de Historia Natural de París (P) se conserva el ejemplar *Riedel 724*, coleccionado en Brasil, que probablemente corresponda a un isótipo de *Paspalum erianthum* (véanse las observaciones bajo *P. ammodes*).

Los materiales *Gardner 3542* y *Glaziou 22589*, que fueron determinados por Hackel como *Paspalum brevipilum* (en herbario), presentan espiguillas con pilosidad más corta sobre la gluma superior y lemma inferior que lo observado más frecuentemente en la especie.

Trinius (1826) describe a *Paspalum sanguinolentum* y distingue a esta especie básicamente por tener inflorescencias con pocos racimos, espiguillas distribuidas en 2–3 series, cañas erectas, simples con hojas basales y de color atrosanguínea. El análisis del material tipo y de numerosos ejemplares permitió determinar que no existen caracteres para considerar a esta especie como un taxón independiente.

Swallen (1967) describe para el grupo Eriantha de *Paspalum* 10 especies, sobre la base de ejemplares únicos o de pocos especímenes, estos últimos usualmente de la misma localidad, da descripciones breves para cada taxón y no indica las afinidades entre los mismos. Este autor proporciona una clave para distinguir los taxones sobre la base de caracteres relacionados con la forma y pilosidad de las hojas y tamaño de las espiguillas. Como se indicó anteriormente esta especie es marcadamente variable en la pilosidad de los órganos vegetativos, como así también en el tamaño de la espiguilla. Filgueiras (1993) al tratar las especies descritas por Swallen, considera que *P. mollifolium*, *P. sericatum* y *P. formosulum* son indistinguibles de *P. sanguinolentum* y los incluye en la sinonimia de esta última especie; mientras que trata a *P. rigens*, *P. intosum* y *P. haughtii* como sinónimos de *P. erianthum*. Por otra parte, Filgueiras (1993) considera a *P. album* como una especie válida e incluye en su sinonimia a *P. involutum*; caracteriza a esta especie por la presencia de nudos pilosos y por tener pelos en la porción basal de la lámina y la relaciona con *P. erianthoides* por las hojas involutas; sin embargo *P. erianthoides* se distingue por sus hojas filiformes, macizas e inflorescencias subespiciformes. En el presente trabajo se considera que la pilosidad de los nudos y de la lámina son caracteres indistinguibles de otros especímenes de *P. erianthum*; además, el tamaño y forma de las inflorescencias, pilosidad, forma y tamaño de las espiguillas y la presencia de base subbulbosa del ejemplar tipo de *P. album* no permiten diferenciarle de *P. erianthum*.

Guzmán (1982) al describir *Paspalum trichoides* cita como material tipo el ejemplar *E. W. Nelson 2734a* depositado en el herbario US. Al revisar el material depositado en este herbario sólo se halló el ejemplar *Nelson 2735a*, el que coincide con los datos del protólogo. Por ello es posible que el número citado por Gúzman se deba a un error al transcribir la etiqueta del mencionado ejemplar. El ejemplar *Nelson 2735a*, conjuntamente con el número *2735* del mismo colector, fueron citados bajo *P. sanguinolentum* por Chase (1929), y bajo *P. erianthum* por Nash (1912) y Chase (1913).

Guzmán (1982) al describir *Paspalum trichoides* la relaciona con *P. haughtii* (= *P. erianthum*), y caracteriza a la especie por tener espiguillas de color pálido, por la pilosidad poco conspicua de la gluma superior y lemma inferior y por tener brácteas 3-nervias, caracteres que no permiten diferenciar a la especie de *P. erianthum*.

De acuerdo a Rosengurtt et al. (1970) y Smith et al. (1982) es un forraje apetecido, poco productivo.

Material adicional examinado. ARGENTINA. **Corrientes:** Dpto. Santo Tomé, Ruta Prov. 40, 4 km de Azara camino a Garruchos, cerca del Río Chimiray, *Morrone et al. 1802* (MO, SI). BOLIVIA. **Beni:** Prov. Yacuma, 96.6 km S de Riberalta, al E del camino Riberalta–Santa Rosa, *Hanagarth & Rosales 149* (LPB, SI). **Santa Cruz:** Ñuflo de Chávez, Ea. San Josecito, 3 km N of Concepción, *Killeen 1139* (LPB, MO, SI). BRASIL. **Ceará:** sin localidad, 1840, *Gardner 1888* (G, K, P, US, W). **Distrito Federal:** Brasília, Lago Sul, *Zuloaga 3836* (SI). **Goiás:** Serra do

Caiapó, ca. 30 km N of Jataí, on road to Caiaponia, *Irwin & Soderstrom 7302* (K, P, US). **Mato Grosso:** ca. 90 km N of Xavantina, *Irwin & Soderstrom 6809* (B, K, MO, SI, US). **Minas Gerais:** campos de Itabira, *Glaziou 17939* (G, K, P, W). **Paraná:** Ponta Grossa, *Swallen 8458* (MO). **Rio de Janeiro:** sin localidad, 1885, *Glaziou 15635* (G, K, P, US, W). **São Paulo:** Casa Branca, *Chase 10584* (MO, W). COLOMBIA. **Meta:** 20 km SE Villavicencio, *Killip 34323* (US). HONDURAS. **Comayagua:** along Hwy. CA-5, 12 km E of Siguatepeque, *Pohl & Davidse 12039* (MO). **Olancho:** Mun. La Unión, ca. 10 mi. E of La Unión along road to Olanchito, *Davidse et al. 35467* (MEXU, MO). MÉXICO. **Oaxaca:** vicinity of San Juan Guichicovi, *Nelson 2735* (US). NICARAGUA. **Matagalpa:** Cerro El Apante Grande, ca. 2 km al S de Matagalpa, *Soza et al. 118* (MO). PARAGUAY. **Amambay:** "in altaplanitie et declivibus Sierra de Amambay", *Hassler 10765a* (BM, K, US). VENEZUELA. **Barinas:** cercanías de Barinas, carretera a San Silvestre, *Ramia 1145* (MO).

4. **Paspalum guttatum** Trin., Gram. Panic.: 91. 1826. TIPO: Brasil. Minas Gerais: Barra do Jequitiba, nov. 1824, *G. H. von Langsdorff s.n.* (holótipo, LE-TRIN-0468.02!; isótipos, LE!, US-2855317!; probable isótipo, *L. Riedel s.n.*, K!, P!). Figura 7.

Plantas perennes, con rizomas rígidos, de entrenudos cortos; *cañas* de (40–)50–90 cm de alto, 0.2–0.3 cm de diámetro, erectas; entrenudos 2–3, de 15–25 cm de largo, cilíndricos a comprimidos, glabros, huecos; nudos glabros a pilosos, castaños. *Vainas* más cortas que los entrenudos, predominantemente basales, persistentes en la base, laciniadas, fibrosas, protegiendo la base, glabras a hirsutas, los márgenes glabros a pestañosos; *lígulas* de 0.2 mm de largo; pseudolígula formada por un arco de pelos densos hasta de 0.5 mm de largo; cuello glabro; *láminas* lineares, de 10–30 cm de largo, 0.2–0.4 cm de ancho, planas a involutas, predominantemente basales, reducidas hacia el ápice de las cañas, las más viejas espiraladas, enrolladas en la base; láminas con la cara adaxial glabra a hirsuta, la abaxial hirsuta, de base atenuada y ápice largamente agudo, los márgenes papiloso-pilosos. *Pedúnculos* largamente exertos, hasta de 45 cm de largo, cilíndricos, glabros; *inflorescencias* terminales, de 3–8 cm de largo, 2–8 cm de ancho; eje principal nulo; racimos 2, raro 1 ó 3, subconjugados, ascendentes, terminando en una prolongación estéril con espiguillas parcialmente desarrolladas; pulvínulos densamente vilosos, raquis de los racimos de 3–9 cm de largo, 1–1.8 mm de ancho, aplanado, cortamente alado, sinuoso, verdoso a violáceo, glabro a hispídulo, aquillado, con quilla prominente, escabrosa, los márgenes escabrosos; pedicelos hasta de 1 mm de largo, cortamente pilosos; espiguillas solitarias, imbricadas, densamente dispuestas a lo largo del raquis en 2 series. *Espiguillas* elipsoides, de 4–5 mm de largo, 1.5–2 mm de ancho (sin los pelos), de ápice agudo, plano-convexas, densamente vilosas, plateadas, con tintes purpúreos entre los nervios; gluma superior 0.8–1 mm más larga que la lemma inferior, membranácea; *gluma superior* tan larga como la espiguilla, con los márgenes y la porción basal densamente pilosa, con pelos plateados, sedosos, de 4–5 mm de largo, el resto de la superficie esparcidamente pilosa, 5-nervia, con el nervio central y los 2 laterales fuertemente marcados, los restantes tenues, submarginales; *lemma inferior* glumiforme, de 3.8–4 mm de largo, densamente vilosa, 3-nervia; *antecio superior* elipsoide, de 3–3.6 mm de largo, 1.4–1.6 mm de ancho, 0.8–1 mm más corto que la gluma superior, pajizo, cartilaginoso, glabro; lemma con papilas simples distribuidas regularmente y micropelos bicelulares hacia el ápice, 5-nervia, los márgenes enrollados sobre la pálea; pálea de textura similar que la lemma, con papilas verrucosas distribuidas regularmente, cuerpos de sílice y micropelos bicelulares hacia los márgenes apicales; lodículas 2, ca. 0.4 mm de largo; estambres 3, anteras de 2.4–2.6 mm de largo. *Cariopsis* no vista.

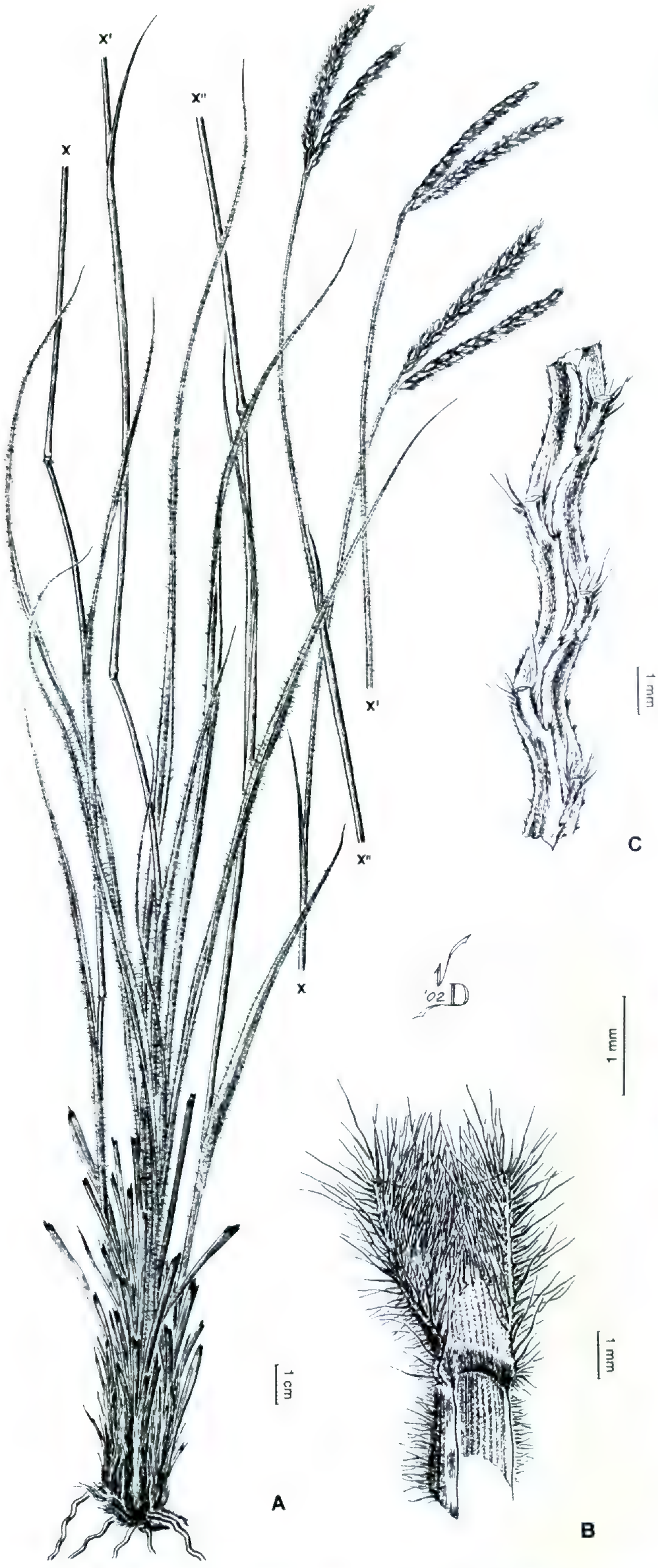
Distribución geográfica y ecología. Crece en Brasil Central, en el Distrito Federal, Goiás, Mato Grosso, Minas Gerais y São Paulo (Fig. 8). Habita en cerrados, en campos o laderas, sobre suelos arenosos, arcillosos o entre rocas, preferentemente entre los 300–1600 m de altura.

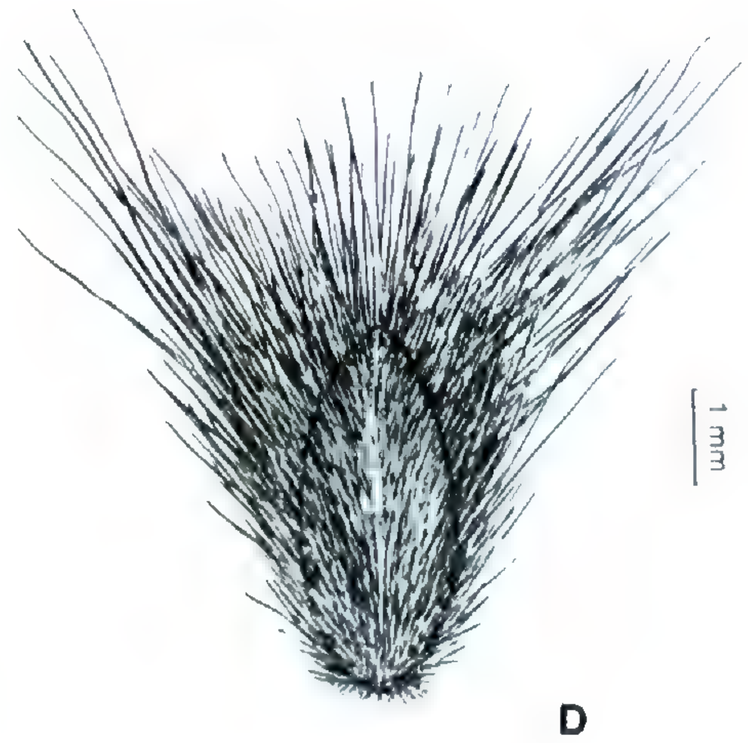
Paspalum guttatum es afín a *P. ammodes* por ser las únicas especies del grupo con espiguillas solitarias, por tener láminas lineares, predominantemente basales, y espiguillas elipsoides a largamente elipsoides y papiloso-pilosas (véanse las diferencias entre estas dos especies bajo observaciones de *P. ammodes*).

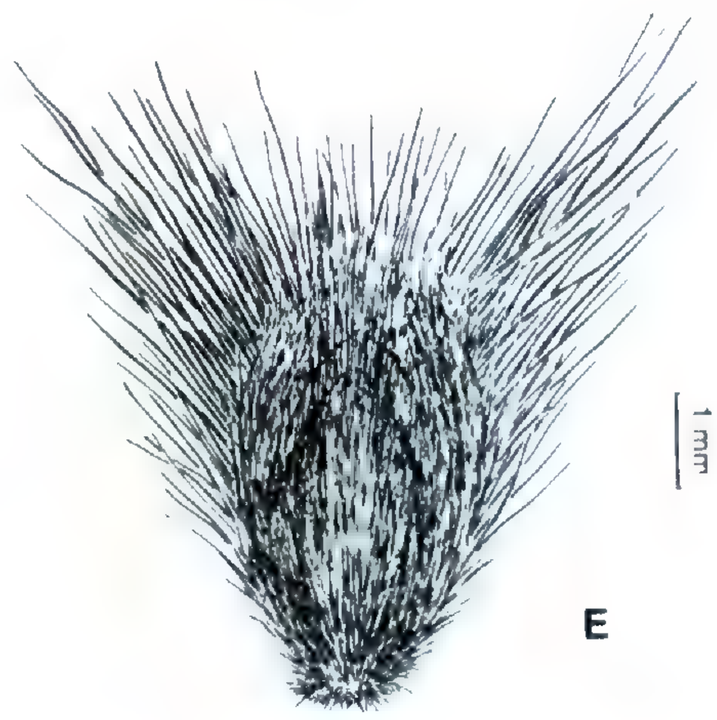
Algunos ejemplares con largos racimos recuerdan superficialmente a *P. eucomum* Nees ex Trin. y la forma de la espiguilla a *P. carinatum* Humb. & Bonpl. ex Flüggé, miembros del subgénero *Ceresia* de *Paspalum*.

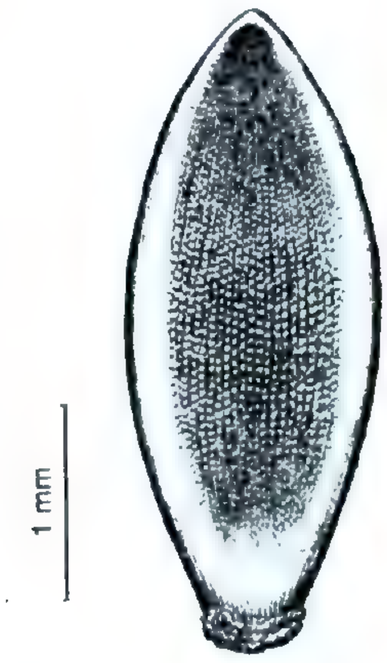
En el Herbario del Museo Nacional de Historia Natural de París (P) y en el Jardín Real Botánico (K) se halló el ejemplar *Riedel s.n.*, coleccionado en Brasil, que probablemente corresponda a un isótipo de *P. guttatum* (véanse las observaciones bajo *P. ammodes*).

Material adicional examinado. BRASIL. **Distrito Federal:** Ponte Alta-Gama, *Allem 309* (MO); betw. Brasília and Sobradinho, *Irwin et al. 9163* (MO, US); Mun. Planaltina, Vale do Amanhecer, *Allem & Vieira 1117* (MO). **Goiás:** sin localidad, *Glaziou 22442* (BM, G, K, P, W); Formoza, Serra de São Pedro, *Glaziou 22467* (K, P, W). **Mato Grosso:** Faz. Urubú Branco, *Pires & Silva*









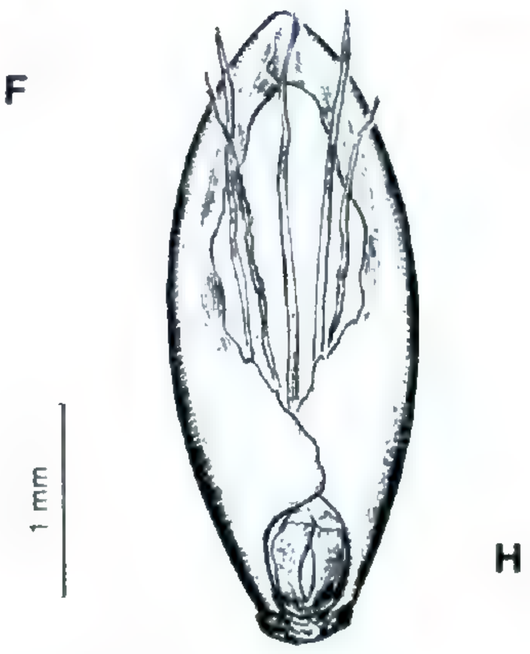


Figura 7. *Paspalum guttatum*.—A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción de racimo. —D. Espiguilla vista del lado de la gluma superior. —E. Espiguilla vista del lado de la lemma inferior. —F. Antecio superior visto del lado de la lemma. —G. Pálea superior, vista dorsal. —H. Pálea superior con lodículas. (A, B, de *Glaziou 22440*; C–H, de *Chase 10312*.)

Figura 8. Distribución de *Paspalum guttatum* y *P. paucifolium.*

11322 (US); vicinity of Xavantina, *Irwin & Soderstrom* 6795 (SI). **Minas Gerais:** Hargreaves, *Chase 10277* (R, W); Serra da Lapa, *Riedel s.n.* (P, US). **São Paulo:** Mun. Botucatu, 18 km N of Botucatu, 14 km E of São Manuel, along the São Manuel–Piracicaba hwy., *Gottsberger 218–31872* (MO); Casa Branca, *Loefgren 1508* (P, US); Mun. Itirapina, 6 km NE of Itirapina, at km 205 on Campinas, São Carlos, *Skvortzov 69* (K, MO, US).

5. **Paspalum paucifolium** Swallen, Phytologia 14: 372. 1967. TIPO: Brasil: sin localidad, *F. Sellow 3541* (holótipo, US-1258166!, foto, SI!; isótipos, B!, P!). Figura 9.

Plantas perennes, con rizomas horizontales, arqueados, viajeros, cubiertos de catáfilos vilosos, con pelos blanquecinos, adpresos; *cañas* de 40–100 cm de alto, 0.2–0.3 cm de diámetro, erectas, paucinodes; entrenudos 2–5, de 7–25 cm de largo, cilíndricos, huecos, glabros; nudos comprimidos, castaños, glabros a pilosos. *Vainas* predominantemente basales, superpuestas, las basales de 1–3 cm de largo, densamente hirsutas, rodeadas de catáfilas en la base, las de las cañas floríferas de 5–15 cm de largo, hirsutas en la porción distal, luego glabras, los márgenes glabros a pestañosos; *lígulas* de 0.5–1.4 mm de largo, de ápice lacerado, glabras; pseudolígula ausente; cuello glabro a piloso, castaño; *láminas* lineares a linear-lanceoladas, de 5–18 cm de largo, 0.3–0.6 cm de ancho, reducidas hacia el ápice de las cañas, predominantemente basales, rígidas, planas, glabrescentes a densamente papiloso-pilosas en ambas caras, con pelos cortos, de base redondeada a subcordada y ápice agudo a subulado, los márgenes escabriúsculos, largamente pestañosos, con pelos tuberculados, blanquecinos, hasta de 6 mm de largo. *Pedúnculos* largamente exertos, hasta de 30 cm de largo, cilíndricos, glabros; *inflorescencias* terminales de 4.5–12 cm de largo, 2–4 cm de ancho; eje principal de 1–6 cm de largo, aplanado, glabro, escabriúsculo a liso; pulvínulos largamente pilosos; racimos 2–4, alternos, ascendentes, distantes entre sí, adpresos a ligeramente divergentes del raquis, terminando en

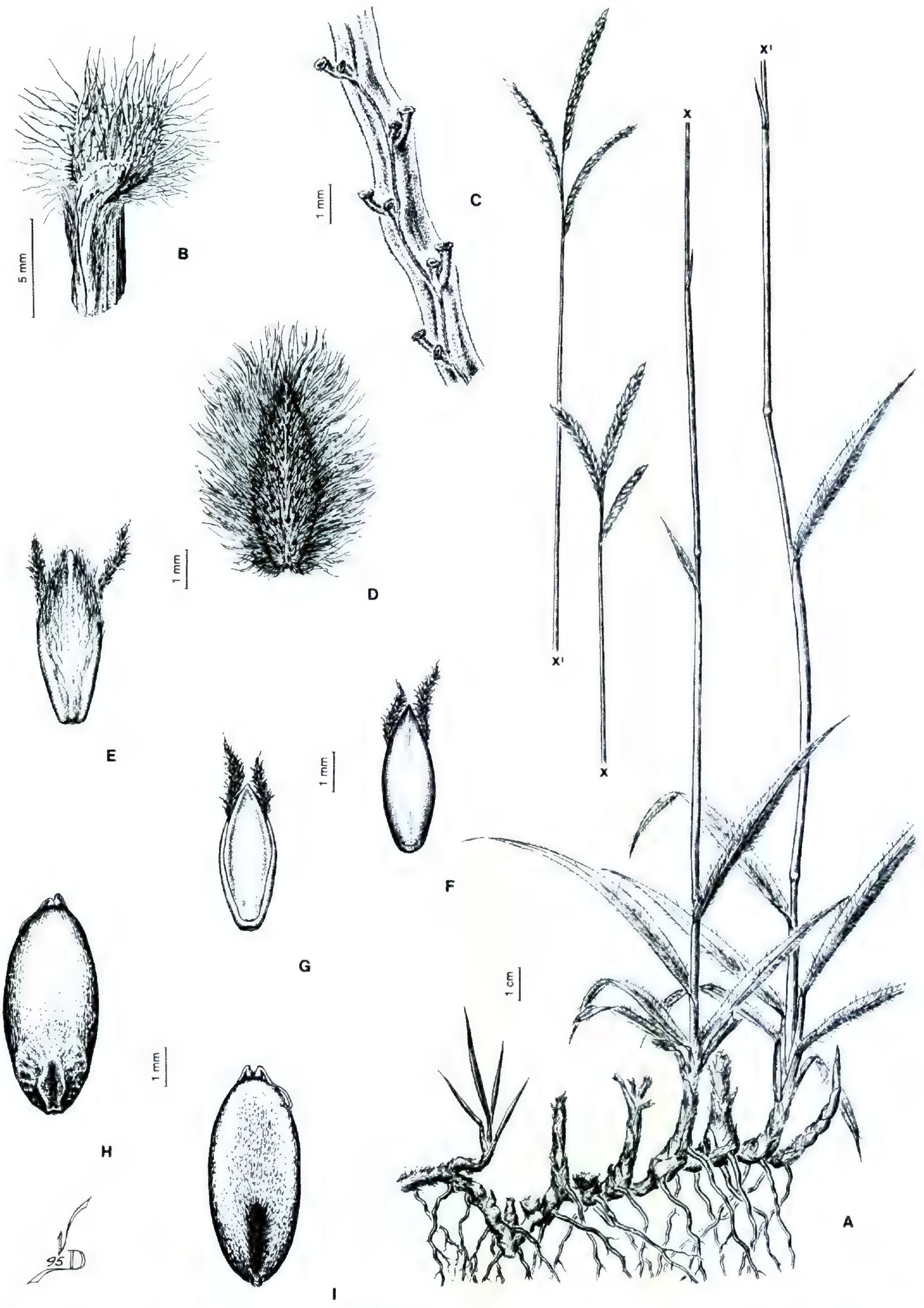


Figura 9. *Paspalum paucifolium.* —A. Hábito. —B. Detalle de la región ligular. —C. Detalle de una porción de racimo. —D. Espiguilla vista del lado de la gluma superior. —E. Lemma inferior con estigmas de la flor superior. —F. Antecio superior visto del lado de la lemma. —G. Antecio superior visto del lado de la pálea. —H. Cariopsis, vista escutelar. —I. Cariopsis, vista hilar. (A, de *Balansa 73*; B–I, de *Burkart 26195.*)

una espiguilla desarrollada; raquis de los racimos de 2–6.5 cm de largo, 1–1.3 mm de ancho, aplanado, glabro, verdoso a violáceo, con los márgenes glabros, escabriúsculos; pedicelos desiguales, hasta de 1.6 mm de largo, escabriúsculos a pilosos, con pelos blanquecinos en los márgenes; espiguillas en pares, en ocasiones la inferior abortada, dispuestas en 4 series. *Espiguillas* largamente elipsoides, de 3.6–5 mm de largo, 1.2–1.8 mm de ancho (sin los pelos), de ápice agudo a acuminado, plano-convexas, papiloso-pilosas, plateadas; gluma superior y lemma inferior subiguales, membranáceas, con los márgenes y la base largamente pilosos, con pelos blanquecinos hasta de 3 mm de largo, la gluma con la región media cubierta por pelos y la lemma con la región media pubescente; *gluma superior* tan larga como la espiguilla, 5-nervia, con un nervio central y los restantes marginales; *lemma inferior* gluminforme, 3-nervia; *antecio superior* elipsoide, de 3–4 mm de largo, 1–1.2 mm de ancho, 0.5–1 mm más corto que la gluma superior y lemma inferior, cartilaginoso, pajizo, finamente papiloso; lemma con papilas simples distribuidas regularmente, macropelos y micropelos bicelulares hacia el ápice, los márgenes enrollados sobre la pálea, 5-nervia; pálea de similar textura que la lemma, con papilas regularmente distribuidas y micropelos hacia los márgenes y el ápice; lodículas 2, ca. 0.3 mm de largo; estambres 3, anteras de 2.4–3 mm de largo, amarillentas. *Cariopsis* elipsoide, de 2.4 mm de largo, 1 mm de ancho; hilo elíptico, 1/3 del largo de la cariopsis; embrión 1/3 del largo de la cariopsis.

Distribución geográfica y ecología. Habita en Brasil, Paraguay, Uruguay y Argentina (Fig. 8), frecuente en campos húmedos, en suelos arcillosos, arenosos o médanos o a lo largo de arroyos.

Nombre vulgar. "Capim-formiga" (Brasil, Smith et al., 1982).

Paspalum paucifolium es afín a *P. erianthum* por compartir ambas especies espiguillas largamente elipsoides, papiloso-pilosas y antecio superior papiloso y con micropelos bicelulares hacia los márgenes apicales. Se distingue de *P. erianthum* por poseer la base rizomatosa, con rizomas viajeros, horizontales, arqueados, cubiertos por catáfilos vilosos, hojas dispuestas en la base rodeadas de catáfilos, inflorescencias con 2 a 4 racimos, y antecio superior 0.5–1 mm más corto que la gluma superior y la lemma inferior.

Swallen (1967) describe a la especie con espiguillas solitarias. El análisis del material tipo y de material de herbario permitió observar que la espiguilla inferior del par se halla reducida y los pedicelos se distribuyen en pares. Es frecuente observar en una misma inflorescencia espiguillas en pares y otros con la espiguilla superior desarrollada y la inferior abortada como en *Balansa 73* y *4360.*

Swallen (1967) al describir *Paspalum paucifolium* cita como holótipo el ejemplar coleccionado por *Sellow* en Brasil, sin indicar número de colecíon. El análisis del holótipo depositado en el herbario US permitió verificar que en el ejemplar se indica claramente que dicho número es *Sellow 3541*; duplicados de esta colección fueron también examinados en B y en P.

Material adicional examinado. ARGENTINA. **Corrientes:** Dpto. San Cosme, Paso de la Patria, *Quarín 3028* (SI); Dpto. Mburucuyá, Estancia Santa María, *Pedersen 4552* (MO); Dpto. Empedrado, Lomas de Empedrado, *Pedersen 9679* (MO). **Entre Ríos:** Palmar Grande de Colón, *Burkart 20571* (SI); ruta 14, bañados del Río Mocoretá, *Nicora 5746b* (SI); Federación, Santa Ana, *Burkart & Troncoso 26195* (SI, US). BRASIL. **Rio Grande do Sul:** Pelotas, *Swallen 9162* (US); São Jeronimo, Fazenda do Leão, *Barreto 829* (SI); Uruguaiana, *Swallen 7643* (MO, US). PARAGUAY. **Amambay:** Sierra de Amambay, "in campis altis Peguahó", *Hassler 11989* (G); zwischen Río Apa und Río Aquidabán, Caballero Cué, *Fiebrig 4908* (BM, G, K). **Central:** near Villeta, *Pedersen 9503* (K, P); Campo Grande, entre Luque et La Trinidad, *Balansa 73* (G, K, P). **Guairá:** Itapé, *Balansa 73a* (P). **Paraguarí:** sin localidad, oct. 1882, *Balansa 4360* (P); Caapucú, Estancia Barrerito, *Rojas 13164* (CTES). URUGUAY. **Artigas:** Río Uruguay y Arroyo Ñaquiná, Estancia Ezequiel Palma, *Izaguirre 1970* (CTES); Río Uruguay y Ayo. Hacumbú, *Rosengurtt et al. 10513* (CTES).

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Apéndice 1.

Lista de especies aceptadas del grupo Eriantha de *Paspalum*.

1. *Paspalum ammodes* Trin.
2. *P. erianthoides* Lindm.
3. *P. erianthum* Nees ex Trin.
4. *P. guttatum* Trin.
5. *P. paucifolium* Swallen

Apéndice 2. Índice de colectores. Cada espécimen es ordenado alfabéticamente por su primer colector. El (#) corresponde a la especie.

Allem 309 (4), 1089 (4), 1117 (4); Altson 7568 (3); Archer 4088 (3).

Balansa 71 (1), 72 (2), 73 (5), 73a (5), 4360 (5); Baldwin 3077 (3); Barreto 829 (5), 887 (5); Beck 20556 (3); Black 2157B (3); Borges 11519 (4); Brito 150 (1); Burch 6206 (3); Burchell 7818 (3), 8005 (3), 8332 (1); Burkart 19732 (2), 20571 (5), 22910 (5), 24722 (5), 26195 (5).

Cabrera 28759 (2); Carnevali 3380 (5); Castellanos 21740 (1); Catal 1332 (1); Chase 9296 (3), 10226 (3), 10244 (3), 10277 (4), 10307 (4), 10308 (4), 10312 (4), 10315 (3), 10323 (3), 10327 (3), 10345 (4), 10347 (1), 10414 (4), 10483 (3), 10509 (3), 10512 (3), 10521 (3),

10525 (4), 10559 (3), 10566 (3), 10584 (3), 10605 (3), 10839 (3), 11731 (3), 11901 (3), 12063 (3) ; Chaves 11648 (1); Cristophel 134 (4).

Davidse 35467 (3); de Campos 113 (3); Dombrowski 2105 (2), 5457 (2), 5650 (2), 6345 (3), 6717 (3); Dusén 1189a (2), 1234a (1), 1354a (3), 2331 (2), 8918 (2), 10413 (3), 10885 (2), 13257 (1), 13543a (3), 15669 (3), 16025 (1), 17409 (3), s.n. (3); Dutra 546 (5).

Eiten 1483 (3), 6749 (3), 9044 (3).

Fiebrig 4908 (5); Filgueiras 766 (4), 2207 (3), 2885 (1); Fonseca 1222 (1); Fróes 30164 (1).

Gardner 1888 (3), 3541 (1), 3542 (3); Glaziou 15635 (3), 16538 (3), 16558 (3), 17373 (3), 17374 (3), 17939 (3), 20556 (3), 20560 (3), 22440 (4), 22442 (4), 22467 (4), 22469 (1), 22471 (1), 22477 (1), 22478 (1), 22489 (3), 22490 (3), 22491 (3), 22492 (3), 22510 (3), 22589 (3), 22608 (3), 22613 (3), s.n. (1); Gottsberger 28–31872 (1), 218–31872 (4).

Hanagarth 149 (3); Harley 10307 (3), 10495 (3), 15466 (1) ; Hassler 9539 (1), 9742 (3), 10673 (2), 10765 (3), 10765a (3), 11377 (2), 11665 (2), 11924 (3), 11941 (2), 11989 (5), 12906 (2) ; Hatschbach 8436 (2), 15356 (2), 27834 (3), 28135 (2), 29202 (2), 29208b (2), 30654 (2), 33188 (3), 35422 (3), 48512a (1) ; Heringer 11629 (3); Hoehne 9741 (4); Huber 10505 (1).

Irwin 6078 (3), 6685 (3), 6701 (3), 6795 (4), 6807 (3), 6809 (3), 7040 (1), 7302 (3), 7395 (1), 7948 (3), 8231 (3), 8382 (3), 8383 (3), 8590 (3), 9138 (1), 9139 (1), 9163 (4), 9197 (3), 9361 (1), 9363 (3), 9506 (1), 9561 (4), 9569 (1), 9603 (3), 9605 (1), 9606 (4), 9814 (3), 9858 (3), 9860 (1), 10259 (3), 10260 (1), 10330 (1), 10332 (3), 10398 (1), 10599 (1), 10635 (1), 10653 (1), 10890 (3), 10891 (3), 20889a (3), 20898 (3), 23560 (3) ; Izaguirre 1970 (5).

Joly 1726 (3); Jonsson 1234a (1).

Killeen 1139 (3), 1194 (3), 1369 (3), 2191 (3), 2781 (1), 2779 (3), 2786 (1), 7039 (3), 7158 (3), 7210 (3), 7743 (1) ; Killip 34323 (3); Klein 3255 (2), 3336 (2), 3728 (2), 4592 (1); Kral 75196 (3), 75910 (3).

Loefgren 149 (3), 193 (3), 1508 (4), 3818 (3).

Macedo 1388 (1), 1401 (3), 2715 (3); Martius s.n. (3); Mattos 8340 (3), 8500 (3); Mimura 558 (3); Mizoguchi 2662 (3); Morello s.n. (1), s.n. (3); Morrone 1802 (3); Mostacedo 2183 (3).

Nelson 2735 (3); Nicora 5746b (5).

Occhioni s.n. (3); Octacilio s.n. (4); Oliveira 374 (1), 857 (3); Orth 1943 (5).

Pedersen 4503 (5), 4552 (5), 9503 (5), 9679 (5); Pires 2842 (3), 11322 (4); Pohl 5051 (3), 5061 (3), 12039 (3), s.n. (3).

Quarín 3028 (5).

Ramia 1145 (3); Ramos 178a (3); Regnell s.n. (3); Renvoize 3066 (2); Riedel 724 (3), 849 (4), 1135 (3), s.n. (4); Rojas 6316 (1), 13164 (5) ; Rondón 2136 (3), 2147 (3); Rosengurtt 10513 (5); Royo Pallarés 178 (5); Rúgolo 1687 (3).

Schinini 10337 (2); Sellow s.n. (3); Semir 375 (4); Sendulsky 393 (3), 437 (1), 452 (1); Shaw s.n. (3); Skvortzov 69 (4); Smith 8278 (2), 8620 (2), 11628 (2), 13323 (2), 13680 (2), 15482 (2), 15630 (2), 15662 (2), 15674 (2), 15693 (2), 15746 (2); Soria 6805a (1); Soza 118 (3); St. Hilaire 90 (3); Steinbach 3543 (3); Swallen 7117 (5), 7643 (5), 8363 (2), 8458 (3), 9162 (5).

Vargas s.n. (3); Viegas 5187 (3), 5953 (3).

Walter 3467 (1); Weddell 2750 (3); Widgren 879 (3), 1149 (4), 1288 (3), s.n. (4); Williams 11873 (1); Wood 13965 (3).

Zardini 52304 (1), 52369 (2); Zuloaga 3066 (2), 3234 (2), 3836 (3), 4676 (3), 4698 (3), 4832 (1).

Apéndice 3.

Índice de nombres científicos.
* sinónimos en itálica

Anachyris, sección 226
Anachyris, subgénero 226
Axonopus 226
Bertoniana, grupo 228, 230
Cabrerae, sección 226
Ceresia, sección 226
Ceresia, subgénero 226, 228, 230, 240
Conjugata, grupo 226
Cymatochloa, sección 226
Dilatata, grupo 226
Emprosthion, sección 226
Eremachyrion, sección 226
Eriantha, grupo 226, 227, 228, **230,** 239
Erianthum, sección 226
Eriolepidium, sección 226
Eupaspalum, sección 226
Fasciculata, grupo 228, 230
Lanigeri, sección 226
Moenchia, sección 226
Opisthion, sección 226
Paspalum 225, 226, 227, 228, 230, 239, 240
P. album 226, 237, 239
P. ammodes 226, 227, 228, **230,** 233, 239, 240
P. bertonii 228
P. blepharophorum 226
P. canum 231
P. carinatum 240
P. conjugatum 226
P. devincenzii 226
P. diamantinum 226, 231, 233
P. dilatatum 226
P. durifolium 226, 230
P. dusenii 234
P. erianthoides 226, 227, 228, 230, **233,** 234, 238, 239
P. erianthum 226, 227, 228, 230, **234,** 237, 238, 239, 244
P. erianthum var. *strictum* 237
P. eucomum 240
P. fasciculatum 228
P. formosulum 226, 237, 239
P. guttatum 226, 227, 228, 230, 231, **240**
P. hassleri 226
P. haughtii 226, 237, 239
P. humboldtianum 226
P. intosum 226, 237, 239
P. involutum 226, 237, 239
P. lilloi 228
P. mollifolium 226, 237, 239
P. ovatum 226
P. paucifolium 226, 227, 228, 230, 234, **242,** 244
P. polyphyllum 226
P. rigens 226, 237, 239
P. rufum 226, 230
P. sanguinolentum 226, 237, 239
P. sericatum 226, 237, 239
P. sordidum 226, 231, 233
P. trichoides 237, 239
Pterolepidium, sección 226
Quadrifaria, grupo 230
Virgata, grupo 230

PHYLOGENETIC ANALYSIS OF THE MADAGASCAN *EUPHORBIA* SUBGENUS *LACANTHIS* BASED ON ITS SEQUENCE DATA[1]

Thomas Haevermans,[2] *Petra Hoffmann,*[3] *Porter P. Lowry II,*[4] *Jean-Noël Labat,*[2] *and Emile Randrianjohany*[5]

Abstract

Euphorbia subg. *Lacanthis* accounts for more than 70% of the *Euphorbia* species in Madagascar. These spiny succulent plants, with about 80 species endemic to the island, include *E. milii* ("Crown-of-Thorns"), which is popular in the worldwide horticultural trade. The genus was last revised by Boissier in 1862, and the taxonomy of the spiny succulents is currently much confused. Using DNA sequence data, phylogenetic relationships within subgenus *Lacanthis* are clarified and the diversification of Madagascan *Euphorbia* is examined. Maximum parsimony and Bayesian approaches are used to analyze ITS sequence data. The results confirm that some African taxa originally included in the subgenus comprise a distinct clade that is not closely related to the monophyletic *Euphorbia* subg. *Lacanthis* s. str., an exclusively Madagascan group whose basally branching lineages comprise species from northern and eastern Madagascar, whereas the more derived clades show a central and southern distribution. This suggests a northern Madagascan origin for subgenus *Lacanthis*, with species in the basally branching groups showing small spine-like stipular formations; other more recently derived spiny forms, such as *E. milii*, colonized the rest of the island, including the drier southern parts.

Key words: *Euphorbia*, Euphorbiaceae, Internal Transcribed Spacers, ITS1, ITS2, 5.8S, *Lacanthis*, Madagascar, molecular phylogenetics.

The taxonomy of *Euphorbia* L. has always been problematic due to the sheer size of the group (ca. 2000 species) and the tremendous range of morphologies seen among members of the genus. This situation is compounded for the succulent spiny taxa (hundreds of species worldwide) because specimens are often fragmentary and poorly preserved, and many taxa were described from living or spirit specimens that have subsequently been lost. Moreover, it is often difficult to obtain material because export of these plants is subject to restrictions (all succulent taxa of *Euphorbia* are listed in CITES appendix I or II, as they include many horticulturally desirable species). In addition, attempts to assess phylogenetic relationships based on morphology are confounded by succulence and other adaptations to extreme conditions, making it difficult to establish homologies for many taxonomically important characters. In view of these difficulties, analyses based on an independent data set, such as molecular markers, may offer insight into the evolutionary history of the succulent members of *Euphorbia*.

The goal of this paper is to clarify the phylogeny of the spiny succulent *Euphorbia* species in Madagascar using DNA sequence data, and thus to pro-

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vide a basis for developing a revised taxonomy of the ca. 80 species (ca. 120 if the infraspecific taxa are included) present on the island (Haevermans, 2003). The spiny succulent *Euphorbia*, which comprise the Crown-of-Thorns (*Euphorbia milii* Des Moul.) and its relatives, have been referred to by a variety of names in the past. Boissier (1862) established *Euphorbia* sect. *Diacanthium* to accommodate the spiny members of the genus, including the spine-shield-bearing species from Africa as well as the Madagascan leafy spiny species. Many authors have accepted this concept, with minor changes concerning its rank and placement within the genus, including Bentham and Hooker (1880), who recognized *Diacanthium* as a subsection within their broadly defined section *Euphorbium*. Gilbert (1987) reassessed the status of Madagascan and African *Diacanthium*, as well as some species previously included in subgenus *Rhizanthium*, which was originally circumscribed to include all the geophytic taxa from various parts of the paleotropics. He placed all the Madagascan species of *Diacanthium* in a new subgenus *Lacanthis* (Raf.) M. Gilbert [based on *Lacanthis* Raf., Fl. Tell. 94 (1837), type: *L. splendens* (Bojer) Raf.], which includes all the spiny taxa (ca. 80 species) as well as about 10 geophytic species (e.g., *E. rubella* from Ethiopia and *E. primulaefolia* from Madagascar); the spine-shield-bearing species of *Euphorbia* from Africa and India (about 200–300 species) were restricted to subgenus *Euphorbia* (cf. Carter, 1982). Rauh (1995, 1998), however, continued to refer to the Madagascan species as "*Diacanthium*" or the "*E. milii* complex."

Gilbert's (1987) circumscription of *Euphorbia* subg. *Lacanthis* provides a useful hypothesis against which to assess the position of the succulent species in Madagascar within the genus, and to evaluate relationships among the species currently assigned to the group. In this study we have used two approaches to reconstruct a phylogeny based on molecular sequence data from the ITS1 + 5.8S + ITS2 nrDNA region (hereafter referred to as the ITS region): Maximum Parsimony (MP) and Bayesian inference (BI) (Huelsenbeck & Ronquist, 2001; Huelsenbeck et al., 2001). Bayesian analysis has recently been applied in a variety of ways, e.g., paralogy in inferring organismal phylogenies (Martin & Burg, 2002), basal avian divergence (Braun & Kimball, 2002), and human origin (Huelsenbeck & Imennov, 2002).

Materials and Methods

Sampling

The nrDNA regions ITS1, 5.8S, and ITS2 were sequenced for 30 taxa (Appendix 1); sequence data for the remaining 20 taxa were made available by V. Steinmann (Steinmann & Porter, 2002). Two outgroups were chosen from tribe Euphorbieae, subtribe Anthosteminae (a potentially new species of *Anthostema* from Madagascar) and subtribe Neoguillauminiinae (*Calycopeplus casuarinoides* L. S. Sm. from Australia). Their appropriateness as outgroups has been demonstrated by Steinmann and Porter (2002).

The ingroup includes representative taxa of *Euphorbia* subg. *Lacanthis*, as circumscribed by Gilbert (1987), plus a few Madagascan endemics known to be closely allied (Steinmann & Porter, 2002), such as members of section *Deuterocalli* Croizat and section *Denisophorbia* (Leandri) Croizat, as well as *E. emirnensis*, an endemic member (from Madagascar and the Comoros) of subgenus *Esula* Pers. Two species were included as representatives of subgenus *Euphorbia*, *E. drupifera* from Africa and *E. epiphylloides* from India.

DNA Sequencing

Leaf fragments or young green shoots (for leafless plants) were desiccated in the field with silica gel for subsequent DNA extraction (Chase & Hills, 1991). Dried *Euphorbia* material was ground using a Mixer Mill MM 300™ with tungsten carbide beads (from Qiagen Inc.), and the total DNA was extracted with the Dneasy™ Plant kit (Qiagen Inc.) following the manufacturer's protocol (without liquid nitrogen for grinding the plant material). Before PCR, total DNA was purified a second time (to minimize PCR reaction inhibitions) with the Qiaquick™ PCR Purification Kit (Qiagen Inc.).

The entire ITS region (ITS1 + 5.8S + ITS2) was amplified by PCR (28 cycles, 2 min. premelt at 94°C, 1 min. denaturation at 94°C, 1 min. annealing at 50°C, 3 min. extension at 72°C, 7 min. final extension at 72°C) using two primers: AB101F (5'-ACG AAT TCA TGG TCC GGT GAA GTG TTC G-3') and AB102R (5'-TAG AAT TCC CCG GTT CGC TCG CCG TTA C-3') from Sun et al. (1994). Three percent DMSO (1M) was added to the reaction to improve the results.

PCR products were purified with a Concert™ Rapid PCR Purification System, and then cycle-sequenced with the same two primers, with dye terminator and 3% DMSO (1M). Cycle sequencing reactions were purified by ethanol precipitation and run on a PE 3777 automated gel sequencer (Applied Biosystem Inc.) following the manufacturer's protocol.

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSIS

Sequences were assembled and edited using Sequencher® 3 (Genecodes). The resulting matrix was then aligned with the help of POY®, a program that implements the direct optimization and fixed states procedure described in Wheeler (1996, 1999). The resulting matrix was also visually edited with the help of BioEdit® (Hall, 1999).

For the MP and bootstrap resampling (Felsenstein, 1985), the numerous insertion/deletion events (indels) present in the aligned matrix were coded following the method explained in Barriel (1994), and automated using the software Barcod® ver. 1ß2, 02/09/1998. The coding method applied by this software is based on the three following rules: (1) an indel corresponds to a unique mutation event, whatever the number of nucleotides implied, so one indel is treated as equivalent to one character; (2) when many taxa share an indel, the coding system must consider it as a shared state; (3) the coding system must not add any evolutionary steps. This results in the insertion in the matrix of an "I" or "D" (for insertions and deletions), or of "?" (to be interpreted here not as missing data, but as uncertainty, which then could be subsequently optimized).

The "barcoded" matrix was analyzed with PAUP*4.10b for PC (Swofford, 1998) on an AMD Athlon XP1400+ based computer with 256 Mb of RAM. MP analysis was run as follows: heuristic search with tree bisection-reconnection (TBR) branch swapping method, random addition sequence, 1000 replicates, character state optimization set on "accelerated transformation" (ACCTRAN), steepest descent not in effect. Bootstrap resampling was performed as follows: parsimony optimality criterion, 500 replicates with TBR swapping algorithm and holding 10 trees per replicate.

The Bayesian Inference method (BI) used here represents a Maximum Likelihood (ML)-type approach combined with confidence testing expressed in the form of posterior probabilities for the trees obtained in the analyses (Huelsenbeck & Ronquist, 2001). The fundamental distinction between ML and BI is that the latter provides posterior probabilities for the hypotheses tested, not probabilities of data given a hypothesis. The Bayesian analysis was conducted using MrBayes 2.01 (Huelsenbeck & Ronquist, 2001), on an aligned matrix without gap coding, using the HKY85 nucleotide substitution model (Hasegawa et al., 1985), which allows base frequencies to vary, as well as different substitution rates between transversions and transitions.

The analysis of the data set was run using 10^6 generations, which were performed on four Markov chains with trees sampled every 100 generations and with a uniform prior distribution (mcmc ngen = 1000000 printfreq = 100 samplefreq = 10 nchains = 4/lset nst = 2 rates = equal). The Markov chain convergence occurred rapidly (before 1.5 $\times$ 10^4 generations), so in order to ensure subsequent sampling of topologies the first 3000 trees (3 $\times$ 10^4 generations) were discarded as the "burn-in" of the process.

RESULTS

MAXIMUM PARSIMONY

Of 745 total characters, 290 were constant, 109 variable but parsimony uninformative, and 346 potentially parsimony informative. The analysis yielded 809 equally parsimonious cladograms each 1212 steps in length (CI = 0.5652, RI = 0.7142), one of which is shown in Figure 1, with bootstrap resampling values and nodes collapsing in the strict consensus indicated by a dot. The ingroup is monophyletic (BS = 100%). *Euphorbia emirnensis*, a representative of subgenus *Esula*, branches first, followed by *E. pachysantha* (a member of sect. *Denisophorbia* (Leandri) Croizat s.l., BS = 100%). The first part of subgenus *Lacanthis* sensu Gilbert (1987) branches next (BS = 96%); it comprises *E. brunellii* and *E. rubella*, two species from mainland Africa, which form a well supported clade (BS = 100%). The next branch (BS = 96%) comprises the two sampled species of subgenus *Euphorbia* (BS = 100%), followed by the clade representing section *Deuterocalli* (BS = 100%), which lies sister to the *Denisophorbia* + *Lacanthis* s. str. clade and comprises Madagascan sub-aphyllous endemics. The sister group relationship between section *Denisophorbia* s. str. (which includes relatives of *E. pyrifolia*, four of which are sampled here) and subgenus *Lacanthis* s. str. is only moderately supported (BS = 68%), and support is likewise limited for the monophyly of subgenus *Lacanthis* s. str. (BS = 60%).

Although the branching pattern within *Euphorbia* subg. *Lacanthis* is weakly supported, several clearly defined clades can be identified (Fig. 1). The first to branch (BS = 83%) comprises species from the northern and eastern parts of Madagascar, divided into two subclades: the first one (the *E. iharanae* clade, BS = 100%) contains *E. capman-ambatoensis* and *E. iharanae*, and the second one (the *E. thuarsiana* clade, BS = 65%) has four spe-

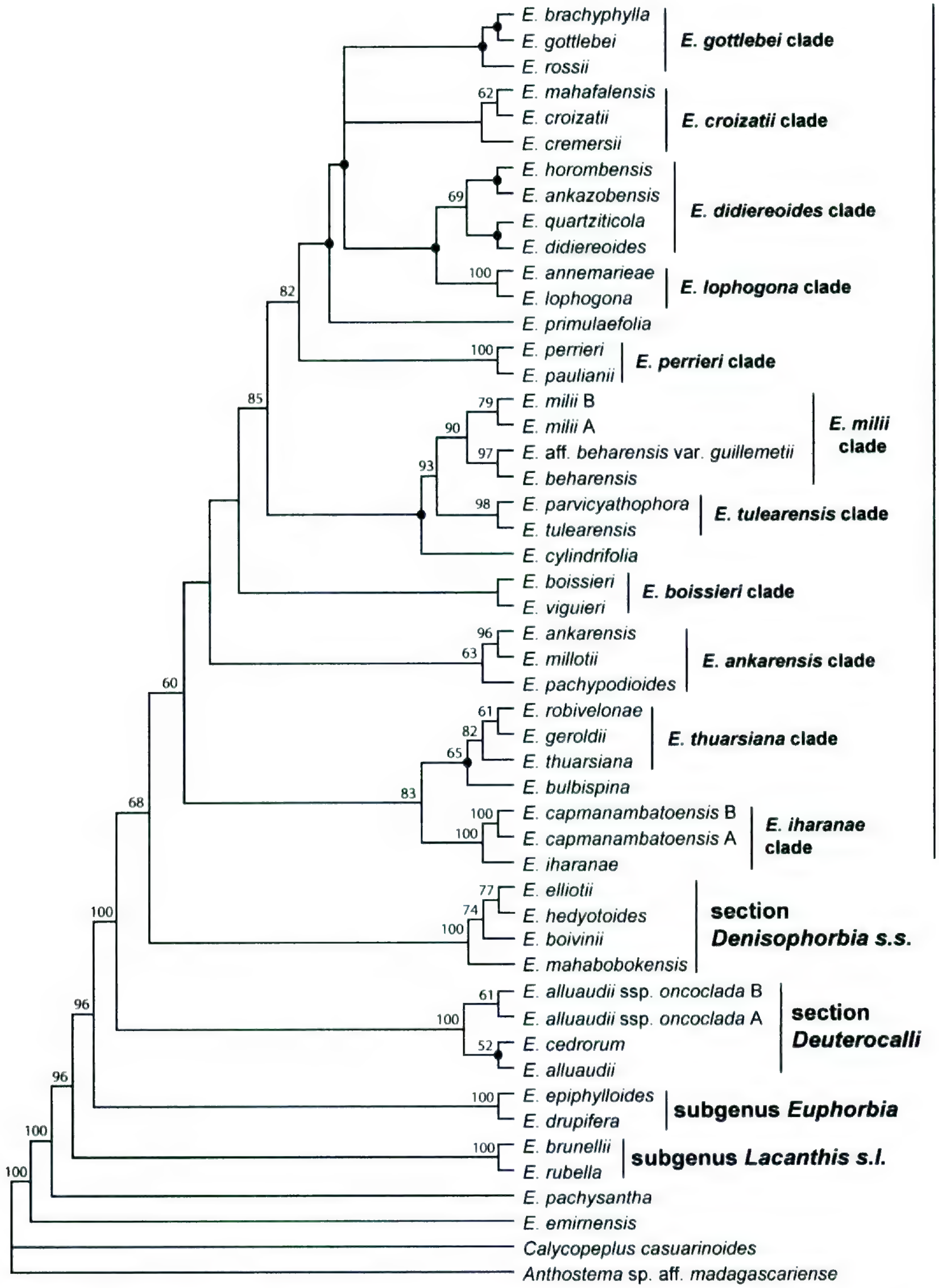

Figure 1. One of the 809 most parsimonious cladograms with a length of 1212 steps (CI = 0.5652, RI = 0.7142). Bootstrap resampling values are given above the supported branches; nodes collapsing in the strict consensus tree are indicated by a dot. (*Euphorbia emirnensis* is in *E.* subg. *Esula*, *E. pachysantha* is in *E.* sect. *Denisophorbia*.) (Only BS greater than 50% are given.)

cies, one of which, the spiny *E. bulbispina* Rauh, branches first, with three inermous species (*E. robivelonae*, *E. geroldii*, and *E. thuarsiana*) then forming a moderately supported subclade (BS = 82%). The next branch within subgenus *Lacanthis* is the *E. ankarensis* clade, which comprises two northern Madagascan species (*E. ankarensis* and *E. millotii*; BS = 96%) that are sister (BS = 63%) to *E. pachypodioides*, whose spines are borne on a podarium (Boiteau, 1947). The *E. boissieri* clade unites the two distinctive monopodial species *E. boissieri* (with inconspicuous erect cyathophylls) and *E. viguieri* (with showy erect cyathophylls), although bootstrap support is weak. This group is sister to a large clade (BS = 85%) containing most of the spiny species of subgenus *Lacanthis*, as well as the Madagascan geophytic taxa. This large group is divided into two unequally supported subclades. The first contains the succulent leafy geophytic species *E. cylindrifolia*, which branches before a clade (the *E. tulearensis* clade, BS = 98%) containing *E. tulearensis* and *E. parvicyathophora* (two other dwarf geophytes), and is sister to the *E. milii* clade (BS = 90%), containing the spiny *E. milii* (BS = 79%) and the closely related *E. beharensis* and *E.* aff. *beharensis* var. *guillemetii* (BS = 97%). The second subclade (BS = 82%), with 15 species, contains the closely related *E. perrieri* (originally misspelled as "*E. perieri*") and *E. paulianii*, forming the *E. perrieri* clade (BS = 100%), which branches basally to a large, poorly resolved clade comprising the remainder of the species sampled from subgenus *Lacanthis*. Within this group, however, four subclades can be seen (Fig. 1), each comprising from two to four species.

BAYESIAN INFERENCES OF PHYLOGENY

The BI tree is given in Figure 2. The overall topology is very similar to that of the MP tree (Fig. 1) but with better node support, and the clades defined in the tree are strongly congruent with morphology. All of the basal nodes have a probability of 1.00 and the value for the sister group relationship between *Euphorbia* sect. *Denisophorbia* s. str. and subgenus *Lacanthis* s. str. is $P = 0.91$. The monophyly of the Madagascan members of subgenus *Lacanthis* is likewise well supported ($P = 0.99$), and in contrast to the MP analysis, most of the internal nodes are satisfactorily supported ($P = 0.91$ to 1.00). The subclade comprising six species (from *E. robivelonae* to *E. iharanae*) is well supported ($P = 1.00$) and its internal structure is best interpreted as a polytomy with three entities: the *E. iharanae* clade ($P = 1.00$), *E. bulbispina*, and the *E. thuarsiana* clade ($P = 1.00$). The basal position of *E. pachypodioides* within the *E. ankarensis* clade ($P = 0.98$) is well supported, and *E. cylindrifolia* is clearly sister ($P = 0.97$) to the lineage ($P = 1.00$) comprising the *E. tulearensis* clade ($P = 1.00$) + the *E. milii* clade ($P = 0.98$). The position of the *E. perrieri* clade is well supported ($P = 1.00$), unlike in the MP analysis. The sister relationship of the *E. lophogona* clade and the *E. didiereoides* clade is well supported ($P = 0.98$), and the latter is clearly monophyletic ($P = 1.00$), although resolution among the four species within the *E. didiereoides* clade is weak. The *E. gottlebei* clade is also well supported ($P = 0.97$), as is the sister relationship of *E. mahafalensis* and *E. croizatii* ($P = 1.00$). For the geophytes, the positions of *E. primulaefolia* and *E. cremersii* are doubtful as the branching patterns are not supported, and in any case they do not appear to be related to the other geophytic species included in the analysis, *E. quartziticola*, which is clearly a member of the *E. didiereoides* clade.

DISCUSSION

POLYPHYLY OF *EUPHORBIA* SUBG. *LACANTHIS* SENSU GILBERT

Gilbert's (1987) circumscription of *Euphorbia* subg. *Lacanthis* encompassed spiny leafy plants (such as *E. milii*), geophytes (e.g., the Madagascan *E. quartziticola* and the Ethiopian *E. rubella*), and sub-inermous rainforest trees (*E. thuarsiana*). Steinmann and Porter (2002) included a few members of *Euphorbia* subg. *Lacanthis* in their study of tribe Euphorbieae and showed that the *E. rubella* group from Africa was not directly related to the Madagascan taxa of *Lacanthis*. Our results, based on an expanded sample of species from Madagascar, with more geophytes, confirm this finding. Both the MP and BI analyses clearly show that the African species included by Gilbert (1987) in subgenus *Lacanthis* are not closely related to those from Madagascar, but rather form a distinct clade that occupies a more basal position within the trees (Figs. 1, 2).

MONOPHYLY OF THE MADAGASCAN MEMBERS OF *EUPHORBIA* SUBG. *LACANTHIS*

The results presented here strongly support the interpretation that the members of *Euphorbia* subg. *Lacanthis* in Madagascar form a well-defined clade. Our expanded sample, comprising 33 of the estimated 80 species in the group (Haevermans, 2003), covers almost all of the morphological and geo-

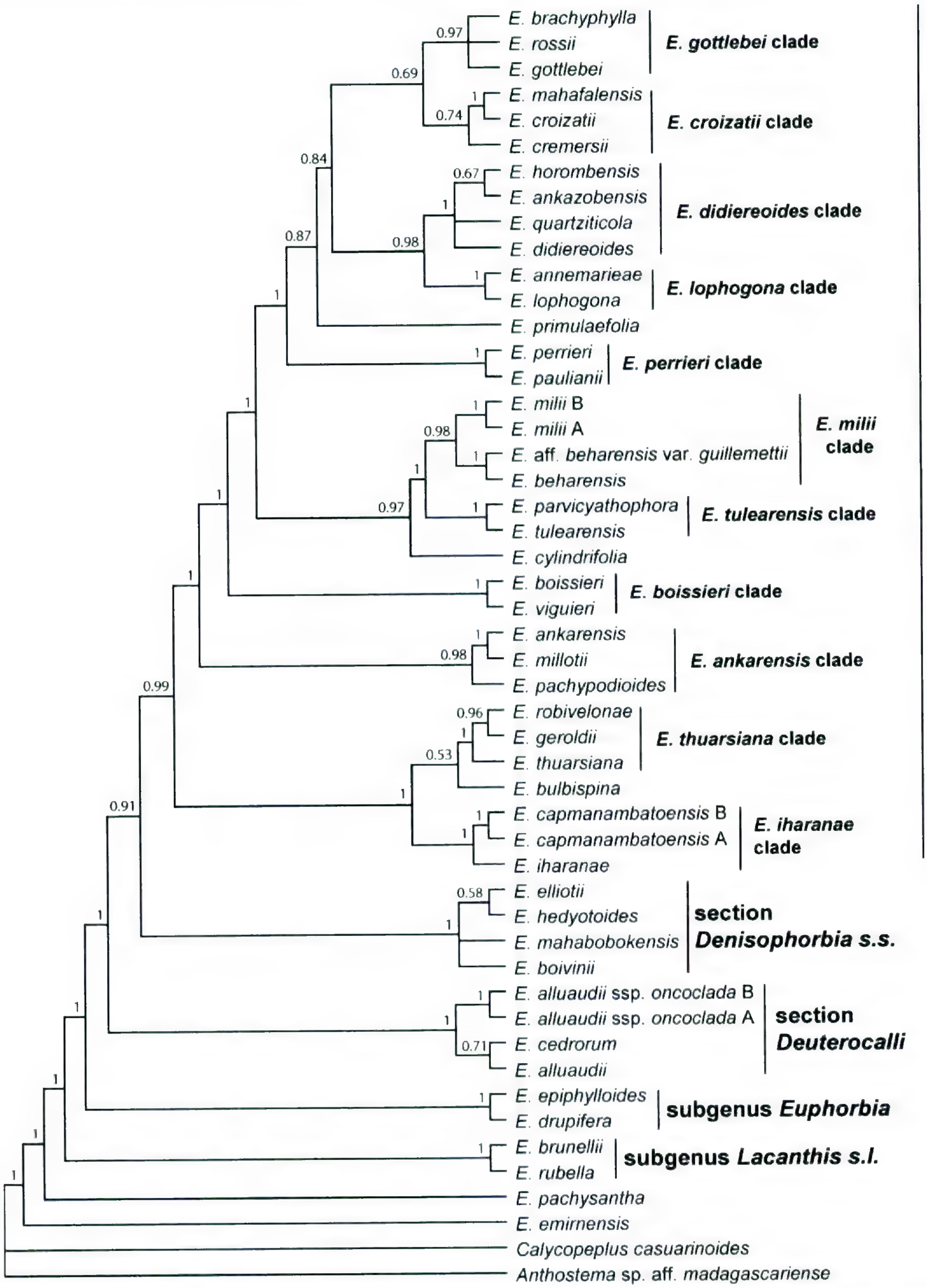

Figure 2. Fifty percent majority rule consensus tree obtained from the Bayesian analysis showing the posterior probabilities for each of the clades. (*Euphorbia emirnensis* is in *E.* subg. *Esula*, *E. pachysantha* is in *E.* sect. *Denisophorbia*.)

graphic variation, leaving little doubt that the lineage evolved in Madagascar from a single common ancestor. It is therefore clear that subgenus *Lacanthis* should be circumscribed more narrowly than originally suggested by Gilbert (1987), and should include only the species from Madagascar. All the Madagascan taxa assigned to the subgenus by Gilbert share a suite of gross cyathial features, whereas the East African species differ in several aspects, most notably in the number of glands (4 + 2) and the pendulous habit of the female flower, although these characters do not offer any insight as to their affinities with the extra-Malagasy species. Including only the Malagasy species, the members of subgenus *Lacanthis* thus appear to have the following morphological synapomorphies: well-developed cyathophylls that are as long as or longer than the cyathium, a consistently hermaphrodite cyathium with 5 equal glands, an erect female flower, and verrucose seeds.

POLYPHYLY OF *EUPHORBIA* SUBG. *RHIZANTHIUM*

As indicated above, the Old World geophytic species of *Euphorbia* were long conceived as forming a group of their own, subgenus *Rhizanthium* (Boiss.) Wheeler (based on sect. *Rhizanthium* Boiss.), regardless of their geographic distribution and anatomy/morphology. The validity of this heterogeneous group was first questioned by Bally (1967), and Gilbert (1987) regarded it as a grade rather than a clade, which prompted him to include some species previously assigned to subgenus *Rhizanthium* within his newly established subgenus *Lacanthis*, dispatching the remaining species to other existing groups. Based on our sampling, which includes eight geophytic species from Madagascar, it is, however, evident that the Madagascan taxa traditionally placed in subgenus *Rhizanthium* do not form a monophyletic group. The geophytes from Madagascar are scattered along the cladogram, some forming a grade basal to the *E. milii* clade, while others are nested within well-supported clades that otherwise do not contain geophytes (e.g., *E. quartziticola* is part of the *E. didiereoides* clade, and *E. cremersii* is a member of the *E. croizatii* clade). It is interesting to note that none of the geophytes sampled here are members of the basal clades within subgenus *Lacanthis* s. str. (i.e., the *E. iharanae*, *E. thuarsiana*, and *E. ankarensis* clades). Moreover, among the species that were not included in our study, there is none likely to be a member of or closely related to these basal clades.

Table 1. Classification of Madagascan spiny succulent *Euphorbia* developed by Ursch and Leandri (1954).

E. ankarensis group	*E. ankarensis* Boiteau
	E. boiteaui Leandri
	E. francoisii Leandri
	E. millotii Ursch & Leandri
E. lophogona group	*E. boissieri* Baill.
	E. leuconeura Boiss.
	E. lophogona Lam.
	E. neohumbertii Boiteau
	E. viguieri Denis
E. milii group	*E. beharensis* Leandri
	E. boiteaui Leandri
	E. brachyphylla Denis
	E. capuronii Ursch & Leandri
	E. decaryi Guillaumin
	E. delphinensis Ursch & Leandri
	E. denisiana Guillaumin
	E. duranii Ursch & Leandri
	E. fianarantsoae Ursch & Leandri
	E. genoudiana Ursch & Leandri
	E. guillemetii Ursch & Leandri
	E. horombensis Ursch & Leandri
	E. leandriana Boiteau
	E. mahafalensis Denis
	E. mainiana Poisson
	E. mangokyensis Denis
	E. milii Des Moul.
	E. quartziticola Leandri
	E. razafinjohanii Ursch & Leandri
	E. tardieuana Leandri
	E. tsimbazazae Leandri
E. pachypodioides group	*E. pachypodioides* Boiteau
E. pedilantoides group	*E. biaculeata* Denis
	E. pedilanthoides Denis
E. perrieri group	*E. caput-aureum* Denis
	E. croizatii Leandri
	E. didiereoides Denis
	E. guillauminiana Boiteau
	E. paulianii Ursch & Leandri
	E. perrieri Drake

RELATIONSHIPS WITHIN *EUPHORBIA* SUBG. *LACANTHIS* SENSU STRICTO

Ursch and Leandri (1954) published the only comprehensive review of the taxonomy of the succulent spiny Madagascan *Euphorbia*, in which they described several species and hybrids based on plants of uncertain origins cultivated in the Parc de Tsimbazaza (Antananarivo, Madagascar). A summary of their classification is given in Table 1. At that time only a small number of Madagascan taxa were known, and the recognition of many new species since then has shown that the informal groups established by Ursch and Leandri (1954) are unsatisfactory. Rauh in particular named many species from Madagascar, and attempted a synopsis of

their classification in two popular books (Rauh, 1995, 1998).

Several authors (Croizat, 1965, 1967, 1972; Cremers, 1984a, 1984b, 1989) have placed the Madagascan species of *Euphorbia* in a series of informal groups on the basis of their gross morphology, although their "groups" might in fact represent grades rather than clades. For example, some species are distinguished by monopodial growth, referred to by Cremers (1984a) as "Euphorbes monocaules," despite the fact that mature individuals eventually exhibit some branching. Species exemplifying this growth form are *E. boissieri*, *E. capmanambatoensis*, *E. lophogona*, and *E. viguieri*. Some other taxa have been assigned to the *E. milii* complex (Rauh, 1995, 1998) and are typically represented by spiny species with showy cyathophylls.

THE *EUPHORBIA IHARANAE* AND *E. THUARSIANA* CLADES

Ursch and Leandri (1954) included *Euphorbia neohumbertii* in their *E. lophogona* group, which unites the monocaulous species and corresponds to the expanded concept of Cremers (1984b). The cladograms presented in Figures 1 and 2 do not, however, support this interpretation, as the monocaulous species do not appear to form a clade. Within subgenus *Lacanthis* s. str. (Figs. 1, 2), the first clade to branch contains monocaulous relatives of *E. neohumbertii* (i.e., *E. capmanambatoensis* and *E. iharanae*) but is sister to the shrub to tree-like inermous relatives of *E. thuarsiana* (*E. tardieuana*, *E. geroldii*, and *E. robivelonae*). These inermous species, initially placed by Ursch and Leandri (1954) in their *E. milii* group, were subsequently thought to belong to *Denisophorbia* (Leandri, 1957), a finding that is not supported by our data.

Among the species possessing true spines, only *Euphorbia bulbispina* was known to occur in the northern part of Madagascar (Rauh, 1998). Its position in a clade containing *E. iharanae* and *E. thuarsiana* (which grow in the same geographical area) has never been proposed before. Despite having spines, *E. bulbispina* is neither a member of the *E. milii* clade nor any of its sister clades, and it possesses a distinct and unique combination of characters (including an obvious hypopodium and the distinctive shape of its spines and cyathophylls), which in light of our molecular results could be reinterpreted to set it clearly apart.

THE *EUPHORBIA ANKARENSIS* CLADE

A similar case is presented by *Euphorbia pachypodioides*, which was placed in a group of its own by Ursch and Leandri (1954) and Rauh (1995). Our cladograms (Figs. 1, 2) show that *E. pachypodioides* (from northern Madagascar) branches basally to the clade comprising *E. ankarensis* and *E. millotii*, two species which also occur in the northern part of the island. *Euphorbia pachypodioides* differs by its cyathophylls, which are distinct but erect like those of members of the *E. ankarensis* group. The position of *E. millotii* was questioned by Rauh (1995), who pointed out the similarity of its stipules with those of *E. thuarsiana*. However, plants of *E. millotii* otherwise resemble *E. ankarensis* and its allies (*E. hermanschwartzii*, *E. denisiana*, *E. alfredii*, not included in the cladogram). The molecular analysis shows that *E. millotii* is not directly related to *E. thuarsiana*, but rather belongs to the *E. ankarensis* clade.

THE *EUPHORBIA BOISSIERI* CLADE

Another pair of distinctive monocaulous species, *Euphorbia viguieri* and *E. boissieri*, were included in this study because their presumed affinities to the other species of *Euphorbia* were highly speculative. *Euphorbia viguieri* has individual, multibranched spines with a thick base (whereas the stipular formations of *E. boissieri* are soft and fleshy, branched combs), and it possesses incyathescences (i.e., cyathia borne in a kind of synflorescence) very similar to those of *E. capmanambatoensis*, with the same large, showy, erect cyathophylls (whereas those of *E. boissieri* are reduced and inconspicuous). For this reason, Rauh (1995) considered *E. viguieri* a member of his *E. neohumbertii* group (also containing *E. capmanambatoensis* and *E. aureoviridiflora*). This view is refuted by the molecular analysis presented here, as *E. boissieri* and *E. viguieri* are likely to be more related to each other, forming their own group, than to the other groups of species.

Euphorbia boissieri is a poorly known species that was until recently known only from a single collection made in 1852 on the Ile Sainte-Marie, off the east coast of Madagascar. It was long considered extinct because its habitat, a single forest on the island, had supposedly been totally destroyed. No other collections of *E. boissieri* were made until it was rediscovered in 2001 in the western part of the Masoala Peninsula, extending the distribution well to the north of the type locality (Haevermans, 2003). The taxonomic position of *E. boissieri* had long been doubtful because of its reduced, inconspicuous cyathophylls, a unique occurrence in subgenus *Lacanthis*. Ursch and Leandri (1954), basing their argumentation on its monocaulous habit, suggested that *E. boissieri* was closely related to *E. lophogona*, but our molecular analyses

refute this, showing instead its relationship to *E. viguieri*.

THE *EUPHORBIA MILII* AND *E. TULEARENSIS* CLADES

The spiny Madagascan euphorbs, often referred to as the *E. milii* complex, are best represented by the well-known *E. milii* and its varieties and hybrids. To date, however, no attempts have been made to identify its closest relatives within subgenus *Lacanthis*. Our molecular data (Figs. 1, 2) indicate that *E. milii* is closest to the succulent leafy, shrubby, spiny *E. beharensis* and *E.* aff. *beharensis* var. *guillemettii* (*E. milii* has thin, soft leaves).

Sister to this group (Figs. 1, 2) are the various geophytic species growing in southern Madagascar (e.g., *E. tulearensis* and *E. parvicyathophora*), which have the same type of succulent leaves with undulate margins as *E. beharensis* and its varieties. This interesting assemblage of dwarf geophytic species [*E. tulearensis*, *E. parvicyathophora*, and *E. cylindrifolia* (herein shown in Figs. 1, 2), but also *E. francoisii*, *E. capsaintemariensis*, and *E. decaryi*, not included in the present study] has been regarded as a group of uncertain affinities. Ursch and Leandri (1954) included *E. francoisii* in their *E. ankarensis* group, but this species shows distinct cyathial and habit features that more likely unite it with the dwarf geophytes from southern Madagascar. Croizat (1972) later established section *Rhizanthopsis*, typified by *E. francoisii*, as a formal name for Ursch and Leandri's *E. ankarensis* group. Rauh (1998) placed these species in a group of their own (including *E. ambovombensis*, *E. capsaintemariensis*, *E. cylindrifolia*, *E. decaryi*, *E. francoisii*, *E. parvicythophora*, and *E. tulearensis*), which he linked to the spiny *E. milii* complex through *E. tulearensis* and *E. parvicyathophora* based on their spine-like stipular structures. Cremers (1984b) included Rauh's species, along with *E. primulaefolia* and *E. moratii*, in his broad concept of "geophytic euphorbs," equivalent to Boissier's section *Rhizanthium*.

As suggested by Rauh (1998), *Euphorbia tulearensis* and *E. parvicyathophora* are closely related to *E. milii*, and they form a clade sister to the *E. milii*/*E. beharensis* clade. This informal group of small succulent plants identified by Rauh is more likely a grade basal to the *E. milii* alliance than a true clade, as *E. cylindrifolia* branches basally in the *E. milii* clade (Figs. 1, 2). The other spiny species thought to be directly related to *E. milii* (Ursch & Leandri, 1954; Rauh, 1998), and thus derived from the same ancestors as *E. cylindrifolia* (and relatives), are more likely to form a distinct clade (Table 1, Figs. 1, 2).

THE *EUPHORBIA PERRIERI* CLADE

Euphorbia paulianii and *E. perrieri* are very closely related (Figs. 1, 2), but their affinities with the other representatives of the genus were previously unknown. These two species are similar in growth form and possess distinctive upright cyathophylls surrounding the cyathium, sharing an overall resemblance with those of *E. pachypodioides* (from the north) and *E. didiereoides* (from the central high-plateau). However, they differ from *E. pachypodioides* and *E. didiereoides* in the morphology of their spines and incyathescences. The *E. perrieri* group, as originally defined by Ursch and Leandri (1954) (Table 1), is too comprehensive and it would be more appropriate to restrict the group to *E. paulianii* and *E. perrieri* only, so that it corresponds to the *E. perrieri* clade indicated in Figures 1 and 2. This is consistent with the suggestion made by Rauh (1995), and reflects the fact that these two species are the only members of the subgenus to possess campanulate cyathia with erect cyathophylls.

THE *EUPHORBIA LOPHOGONA*, *E. DIDIEREOIDES*, *E. CROIZATII*, AND *E. GOTTLEBEI* CLADES

Evaluation of the affinities of the remaining species in the *Lacanthis* s. str. clade is more difficult due to low support at a number of nodes (Figs. 1, 2). The *Euphorbia lophogona* clade is well supported (BS = 100%), confirming the close relationship between *E. lophogona* and *E. annamarieae* pointed out initially by Rauh (1991). The *E. didiereoides* clade (BS = 100%) contains high-plateau species with complex spine patterns (with the exception of *E. quartziticola*, for which the evolution of its geophytic habit appears to have induced a reduction of the stem and of the spine system). The other clades within the terminal part of the MP and BI trees (Figs. 1, 2) are less supported, making it difficult to assess relationships with confidence.

Among these groups, there is, however, a tendency for morphologically quite dissimilar species occurring in the same geographic areas to form clades. For example, the high-plateau species *Euphorbia didiereoides* (spiny bush reaching 2.5 m high), *E. quartziticola* (geophytic species), *E. ankazobensis* and *E. horombensis* (spiny shrubs) form a clade (albeit a moderately supported one) despite their divergent habit and spine and leaf morphologies. *Euphorbia didiereoides* was previously placed in the *E. perrieri* group (Ursch & Leandri, 1954)

because of its distinctive cyathial and stipular spine structure, but Rauh (1995) correctly pointed out that these features have "no evolutive value." All the species found in the *E. gottlebei*, *E. croizatii*, *E. didiereoides*, and *E. lophogona* clades have complex spines, which are absent in *E. perrieri* and *E. paulianii*, as well as in other groups such as the *E. milii* clade.

Geographic Distribution of *Euphorbia* subg. *Lacanthis*

Several interesting patterns can be seen in the geographic distribution of members of *Euphorbia* subg. *Lacanthis*. The shrub to tree-like inermous species, such as *E. thuarsiana* and *E. geroldii*, are restricted to the northeast of Madagascar and do not occur in the drier areas in the western and southwestern parts of the island. *Euphorbia robivelonae* is a riparian species restricted to areas that are flooded on a regular basis, near the northeastern town of Sambava. The clades comprising species with more or less complex spine-like stipular formations, such as *E. milii*, *E. didiereoides*, and *E. lophogona*, are distributed in the central and southern part of the island. The few spiny species from the north (*E. pachypodioides* and *E. bulbispina*, which are restricted to Ankarana and Windsor Castle, respectively, in the far north) are not closely related to the southern spiny species, contrary to what was previously thought, but instead belong to clades also restricted to the north.

The results of our analysis show that the basal clades of *Euphorbia* subg. *Lacanthis* s. str. are composed of taxa from the northeastern part of Madagascar, whereas the derived spiny clades tend to show a central and southern distribution. This suggests a northern origin for the subgenus, with the basal species having minute spiny stipular structures (e.g., as seen in *E. geroldii*). From these forms other spiny taxa such as *E. milii* evolved, diversifying throughout the rest of the island and becoming well adapted to the very dry southern areas. No natural occurrence of the subgenus, as recircumscribed here, has been recorded elsewhere, even on the neighboring island groups such as the Mascarenes and Comoros. *Euphorbia* subg. *Lacanthis* is therefore strictly endemic to Madagascar. Moreover, if the trend toward recognizing subdivisions of *Euphorbia* as distinct at the generic level is accepted (see Gilbert, 1987), then the members of subgenus *Lacanthis* would certainly qualify as a distinct genus.

Conclusions and Perspective

The circumscription and relationships of *Euphorbia* subg. *Lacanthis* are far more complex than thought previously, and the groups recognized by earlier authors on the basis of gross morphology appear for the most part not to comprise monophyletic assemblages. Instead, the results presented here suggest that closely related species tend to have similar eco-geographical distributions. The features that have traditionally been used to define groups among succulent euphorbs, such as monocauly (Cremers, 1984a) and a geophytic habit (Cremers, 1984b, 1989), are in fact the result of convergences likely reflecting similar environmental pressures. This abundance of convergence, occurring not only in subgenus *Lacanthis* but throughout *Euphorbia* as a whole, suggests that an attempt to build a phylogeny based exclusively on morphological characters is not likely to yield reliable results. It will therefore be essential to pursue additional molecular studies to address the tremendous taxonomic problems posed by this huge genus.

The hypothesis of a northern Madagascan origin of *Euphorbia* subg. *Lacanthis* s. str., as well as a narrower circumscription of the group, should now be tested by identifying and analyzing one or more plastid or mitochondrial genes, and by including a broader species sampling in order to produce a robust classification that reflects phylogenetic relationships.

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Appendix 1. Herbarium vouchers and GenBank accession numbers for taxa in this study. Novel GenBank accession numbers submitted by TH are indicated by an asterisk (*); the remainder were made available by Victor Steinmann (cf. Steinmann & Porter, 2002). For herbarium vouchers, "nat." refers to the country of origin. *BGH* represents the Heidelberg Botanic Garden. Epithet terminations were corrected (ICBN, 1999) to *E. boivinii* (from Boivin, Rec. 60C. 1[b]), to *E. paulianii* (for the type collector M. R. Paulian, Art. 60.11, Rec. 60C.1), and to *E. perrieri* (rejecting "perieri" as a typographic error under Art. 60.1).

Taxon	Origin and herbarium voucher	GenBank accession number
Anthostema sp. aff. *madagascariense* Baill.	Madagascar, *Miller et al. 8840* (MO)	AF537583
Calycopeplus casuarinoides L. S. Sm.	Cultivated (nat. Australia), *Steinmann 1407* (RSA)	AF537580
Euphorbia aff. *beharensis* var. *guillemetii* (Ursch & Leandri) W. Rauh	Cultivated (nat. Madagascar), *Rauh 72744* (HEID)	AJ508970*
Euphorbia alluaudii Drake	Madagascar, *Haevermans 48* (P, TAN)	AJ508969*
Euphorbia alluaudii subsp. *oncoclada* (Drake) Friedmann & Cremers, accession A	Madagascar (Toliara), *Haevermans 137* (P, TAN)	AJ508968*
Euphorbia alluaudii subsp. *oncolada* (Drake) Friedmann & Cremers, accession B	Madagascar (Fianarantsoa), *Haevermans 25* (P, TAN)	AJ508967*
Euphorbia ankarensis Boiteau	Cultivated (nat. Madagascar), *Steinmann 1482* (RSA)	AF537462
Euphorbia ankazobensis W. Rauh & Hofstätter	Cultivated (nat. Madagascar), *Rauh s.n. BGH 140151* (HEID)	AF508966*
Euphorbia annamarieae W. Rauh	Cultivated (nat. Madagascar), *Rauh 7557* (HEID)	AJ508965*
Euphorbia beharensis Leandri	Cultivated (nat. Madagascar), *Rauh 72078* (HEID)	AJ508983*
Euphorbia boissieri Baill.	Madagascar (Masoala), *Labat 3355* (P, TAN, TEF)	AJ508963*
Euphorbia boivinii Boiss.	Madagascar (Masoala), *Haevermans 235* (P, TAN, TEF)	AJ508962*
Euphorbia brachyphylla Denis	Cultivated (nat. Madagascar), *Rauh 74943b* (HEID)	AJ508961*
Euphorbia brunellii Chiov. apud Chiarugi	Cultivated (nat. east tropical Africa), *Steinmann 1495* (RSA)	AF537486
Euphorbia bulbispina W. Rauh	Cultivated (nat. Madagascar), *Rauh 68664* (HEID)	AJ508960*
Euphorbia capmanambatoensis W. Rauh, accession A	Cultivated (nat. Madagascar), *Rauh 74546* (HEID)	AJ508959*
Euphorbia capmanambatoensis W. Rauh, accession B	Cultivated (nat. Madagascar), *Steinmann 1468* (RSA)	AF537476
Euphorbia cedrorum W. Rauh & Hebding	Madagascar (Toliara), *Haevermans 81* (P, TAN)	AJ508958*
Euphorbia cremersii W. Rauh & Razafindratsira	Cultivated (nat. Madagascar), *Haevermans s.n.* (P)	AJ508957*
Euphorbia croizatii Leandri	Cultivated (nat. Madagascar), *Rauh 72182* (HEID)	AJ508956*
Euphorbia cylindrifolia Marnier-Lapostolle & W. Rauh	Madagascar, *Haevermans 68* (P, TAN)	AJ508955*
Euphorbia didiereoides Denis ex Leandri	Madagascar, *Haevermans 54* (P, TAN)	AJ508954*
Euphorbia drupifera Thonn.	Cultivated (nat. Africa), *Steinmann 1488* (RSA)	AF537480
Euphorbia elliotii Leandri	Madagascar, *Dorr et al. 3985* (MO)	AF537478
Euphorbia emirnensis Baker	Madagascar (Ankaratra), *Haevermans 95* (P, TAN)	AJ508964*
Euphorbia epiphylloides Kurz	Cultivated (nat. Andaman Islands), *Steinmann 1459* (RSA)	AF537484

Appendix 1. Continued.

Taxon	Origin and herbarium voucher	GenBank accession number
Euphorbia geroldii W. Rauh	Cultivated (nat. Madagascar), *Steinmann 1467* (RSA)	AF537475
Euphorbia gottlebei W. Rauh	Cultivated (nat. Madagascar), *Steinmann 1471* (RSA)	AF537459
Euphorbia hedyotoides N. E. Br.	*Cultivated* (nat. Madagascar), *Steinmann 1472-A* (RSA)	AF537460
Euphorbia horombensis Ursch & Leandri	Cultivated (nat. Madagascar), *Rauh 73701* (HEID)	AJ508971*
Euphorbia iharanae W. Rauh	Cultivated (nat. Madagascar), *Steinmann 1458* (RSA)	AF537477
Euphorbia lophogona var. *tenuicaulis* W. Rauh	Cultivated (nat. Madagascar), *Rauh 74322/ 7 (HEID)*	AJ508972*
Euphorbia mahabobokensis W. Rauh	Cultivated (nat. Madagascar), *Steinmann 1456* (RSA)	AF537522
Euphorbia mahafalensis Denis	Madagascar, *Haevermans 60* (P, TAN)	AJ508973*
Euphorbia milii Des Moul., accession A	Madagascar (Vatovavy), *Haevermans 40* (MO, P, TAN)	AJ508974*
Euphorbia milii Des Moul., accession B	Cultivated (nat. Madagascar), *Steinmann 1476* (RSA)	AF537461
Euphorbia millotii Ursch & Leandri	Cultivated (nat. Madagascar), *Steinmann 1477* (RSA)	AF537463
Euphorbia pachypodioides Boiteau	Cultivated (nat. Madagascar), *Rauh 22871* (HEID)	AJ508975*
Euphorbia pachysantha Baill.	Cultivated (nat. Madagascar), *Rauh 73350* (HEID, P)	AJ508976*
Euphorbia parvicyathophora W. Rauh	Cultivated (nat. Madagascar), *Rauh 74690* (HEID)	AJ508977*
Euphorbia paulianii Ursch & Leandri	Cultivated (nat. Madagascar), *Rauh 73266b* (HEID)	AJ508978*
Euphorbia perrieri Drake	Cultivated (nat. Madagascar), *Steinmann 1483* (RSA)	AF537463
Euphorbia primulaefolia Baker	Cultivated (nat. Madagascar), *Steinmann 1484* (RSA)	AF537466
Euphorbia quartziticola Leandri	Madagascar (Itremo), *Haevermans 6* (MO, P, TAN)	AJ508979*
Euphorbia robivelonae W. Rauh	Cultivated (nat. Madagascar), *Rauh 73927* (HEID)	AJ508980*
Euphorbia rossii W. Rauh & Buchloh	Cultivated (nat. Madagascar), *Steinmann 1449* (RSA)	AF537465
Euphorbia rubella Pax ex Engl.	Cultivated (nat. east tropical Africa), *Steinmann 1464* (RSA)	AF537487
Euphorbia thuarsiana Baill.	Madagascar, *Leeuwenberg & Ranaivojaona 14585* (K)	AF537474
Euphorbia tulearensis (W. Rauh) W. Rauh	Cultivated (nat. Madagascar), *Rauh 68552* (HEID)	AJ508981*
Euphorbia viguieri Denis	Cultivated (nat. Madagascar), *Rauh s.n. BGH 142199*	AJ508982*

HOOGLANDIA, A NEWLY DISCOVERED GENUS OF CUNONIACEAE FROM NEW CALEDONIA[1]

Gordon McPherson[2] *and*
Porter P. Lowry II[2,3]

Abstract

Hooglandia McPherson & Lowry (Cunoniaceae) is described from New Caledonia and recognized as distinct from other Cunoniaceae on the basis of its unique unicarpellate (or perhaps pseudomonomerous) gynoecium, and the combination of dioecy and drupaceous fruit, *inter alia*. The single species, *H. ignambiensis*, known only from primary rain forest on the upper slopes of Mt. Ignambi in northeastern New Caledonia, is assigned a provisional threat status of Critically Endangered.

Key words: conservation, Cunoniaceae, *Hooglandia*, New Caledonia.

Résumé

Description de *Hooglandia* McPherson & Lowry, nouveau genre de Cunoniaceae de Nouvelle-Calédonie se distinguant des autres membres de la famille par un gynécée unicarpellé (éventuellement pseudomonomère) et, *inter alia*, l'association de deux autres caractères: dioicie et fruit drupacé. L'unique espèce, *H. ignambiensis*, n'est connue que de la forêt primaire dense humide des pentes supérieures du Mt. Ignambi, au nord est de la Nouvelle-Calédonie; le statut d'espèce en Danger Critique lui est provisoirement attribué.

New Caledonia is widely recognized for its exceptional botanical diversity, with an estimated seed-plant flora of just over 3000 species, nearly 77% of which are endemic (Lowry, 1998; Jaffré et al., 2001; Morat et al., 2001), qualifying it as a global biodiversity hotspot (Myers et al., 2000). The flora is known for its numerous endemic gymnosperms and representatives of many primitive angiosperm families, including the remarkable genus *Amborella* Baill. (see Soltis et al., 2000; Thien et al., 2003; and references therein).

Recently, while collecting on Mt. Ignambi in the northeast of the island, we encountered first a female and then a male individual of a distinctive tree species, one that matched nothing in our experience. At the time we were unable to place the specimens in any family, despite the fact that we had abundant flowering and fruiting material in hand. Subsequent studies in the herbarium, searches of the literature, and discussions with colleagues confirmed our initial impression that our two collections did, in fact, represent an unusual new element of the flora.

Conspicuous features of the new plant—including its opposite, compound, dentate, stipulate leaves; tetramerous, unisexual flowers; imbricate sepals; lack of a corolla; biseriate stamens; disk adnate to the ovary; unicarpellate (or perhaps pseudomonomerous) gynoecium; and drupaceous, bilaterally symmetrical, one-seeded fruit—suggested, in various combinations, members of the Oxalidales (such as the Cunoniaceae or Brunelliaceae) and the Sapindales (such as the Simaroubaceae, Anacardiaceae, Burseraceae, or Sapindaceae). However, it proved impossible to refer the new taxon to any of the currently recognized genera in these families.

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We were able to place our material only after an analysis of molecular sequence data (Sweeney et al., 2004), which clearly showed that the species belongs within the Cunoniaceae. There it comprises the morphologically well-marked new genus that we describe here. Its closest relative may prove to be *Aistopetalum* Schltr., a genus of two species endemic to New Guinea, which resembles our new genus in its large, paniculate inflorescence, apetalous flowers in which the disk is adnate to the ovary, and indehiscent fruit.

Hooglandia McPherson & Lowry, gen. nov. TYPE: *Hooglandia ignambiensis* McPherson & Lowry.

Genus novum, quoad folia opposita imparipinnata, stipulas interpetiolares, inflorescentias paniculatas, flores tetrameros, androecium diplostemonum, discum intrastaminalem, ovarium superum cum multis aliis Cunoniaceis congruens, sed insigniter carpello unico, natura dioecio, fructu drupaceo monospermo divergens et insuper petalis nullis, disco ovarium adnato insolitum.

Hooglandia shares a number of features with many of the 26 other genera of the family (Bradford & Barnes, 2001; Bradford et al., 2004), including opposite, imparipinnately compound leaves, interpetiolar stipules, paniculate inflorescences, tetramerous flowers, a diplostemonous androecium, an intrastaminal disk, and a superior ovary. However, it is unique among Cunoniaceae in combining a unicarpellate (vs. 2(3–5)-carpellate) gynoecium and a bilaterally symmetrical, drupaceous fruit (vs. typically capsules or follicles, or occasionally (in *Davidsonia* F. Muell., *Schizomeria* D. Don, and *Aistopetalum*) radially symmetrical drupes). As well, most Cunoniaceae are hermaphroditic (22 genera) and have petaliferous flowers (15 genera) with disks free from the ovary wall (20 genera) (Bradford et al., 2004), whereas *Hooglandia* uniquely combines dioecy, a condition it shares with *Pancheria* Brongn. & Gris, *Spiraeanthemum* A. Gray, *Vesselowskya* Pamp., and some *Weinmannia* L. spp., with apetalous flowers in which the disk is adnate to the ovary. The phylogenetic implications of the distinctive characters exhibited by *Hooglandia* are discussed by Sweeney et al. (2004).

The new genus joins 104 other seed-plant genera endemic to New Caledonia (Jaffré et al., 2001), bringing the level of generic endemism to 15%.

Etymology. The genus is named in honor of Ruurd Dirk Hoogland (1922–1994), who devoted much of his career to the study of the Cunoniaceae and Dilleniaceae while serving as a member of the CSIRO New Guinea Group and later at the Australian National University, and then after his retirement at the Muséum National d'Histoire Naturelle in Paris (see Morat, 1995). Ru Hoogland was an excellent collector and an expert on the floras of New Guinea, Norfolk Island, and Lord Howe Island.

Hooglandia ignambiensis McPherson & Lowry, sp. nov. TYPE: New Caledonia. Province Nord: Mt. Ignambi, SW of Tchambouenne, 20°27′35″S, 164°35′41″E, 1150 m, 4 May 2002, *P. P. Lowry II, G. McPherson, T. Le Borgne & R. Pouytiela 5767* (holotype, P; isotypes, CANB, G, MO [2 sheets], NOU). Figure 1.

Arbor dioica, 6–8 m alta. Ramuli novelli pubescentes glabrescentes; internodia cava. Folia imparipinnata opposita decussata 26–37 cm longa; foliola (11–)17–19 opposita chartacea oblonga vel subobovata (5.5–)6–10.8 × (2–)2.5–3.3 cm; lamina matura fere glabra, basi obtusa, margine integra vel sparsim dentata, apice acuminata, nervis utroque costae latere 11–14(–16); petioluli 4–6 mm longi pubescentes; petioli 6.5–9.5 cm longi, 2–3.5 mm diametro; stipulae interpetiolares lineares 8–10 mm longae interdum partitae pubescentes caducae, cicatrice ca. 1.5–3 mm lato. Inflorescentiae axillares paniculatae pubescentes, unusquisque axibus primariis 3 ascendentibus vel recurvatis, in plantis femineis (1–)1.5–4.5 cm, in plantis masculis ad 8 cm longis; bracteae triangulatae 1.5–4 mm longae; cymulae flores 4–6 gerentes; bracteolae 0.8–2 mm longae caducae; pedicelli 0.3–1.5 mm longi articulati, in parte inferiore pubescentes, in parte superiore glabri. Flores masculi: sepala 4 discreta alba imbricata 2.5–3.5 mm longa, 2.5–3 mm lata, subinerassata, extus glabra, intus villosa, ciliata; petala nulla; stamina 8(–9) sub anthesi 4 mm longa, filamenta 3 mm longa subcomplanata, antherae 1 mm longae polliniferae dorsifixae versatiles biloculatae dehiscentia longitudinali latrorsa; discus intrastaminalis basim ovarii adnatus annularis; pistillodium (cum stylo) ca. 1.5 mm altum; loculus et ovula vestigiales; stigma minuta. Flores feminei: perianthium ut in floribus masculis; staminodia 8(–9) sub anthesi 1–1.5 mm longa, antherae 0.5–0.75 mm longae quasi non polliniferae; discus intrastaminalis basim ovarii adnatus annularis; gynoecium carpello unico, ovarium superum viride subcomplanatum 1 mm altum, 1 mm latum, uniloculatum glabrum quasi quadratum ambitu, stylus et umbo apicales, stylus albus linearis adpressus geniculatus, ca. 1 mm longus, apex stigmaticus elongatus; ovula 2, apicalia, anatropa. Fructus axillaris infra inflorescentias, in axibus 3.6–6 cm longis, drupaceus, quasi obovatus vel ellipticus, complanatus, 3.8–4.2 cm longus, 2–2.2 cm latus, 0.5 cm crassus, apice rostellato et umbone ca. 5–6 mm diametro, exocarpium carnosum, endocarpium durum. Semen unicum, testa tenuis, endospermium amylaceum, radicula recta, ca. 5 mm longa, cotyledones complanatae virides, ca. 18 mm longae, ca. 11 mm latae.

Dioecious, unarmed, sparsely branched, odorless trees ca. 6–8 m tall. Twigs densely pubescent with short, subappressed trichomes when young, glabrescent, with scattered lenticels, lacking evident exudates; leaf scars cordiform, 5–6(–10) mm long,

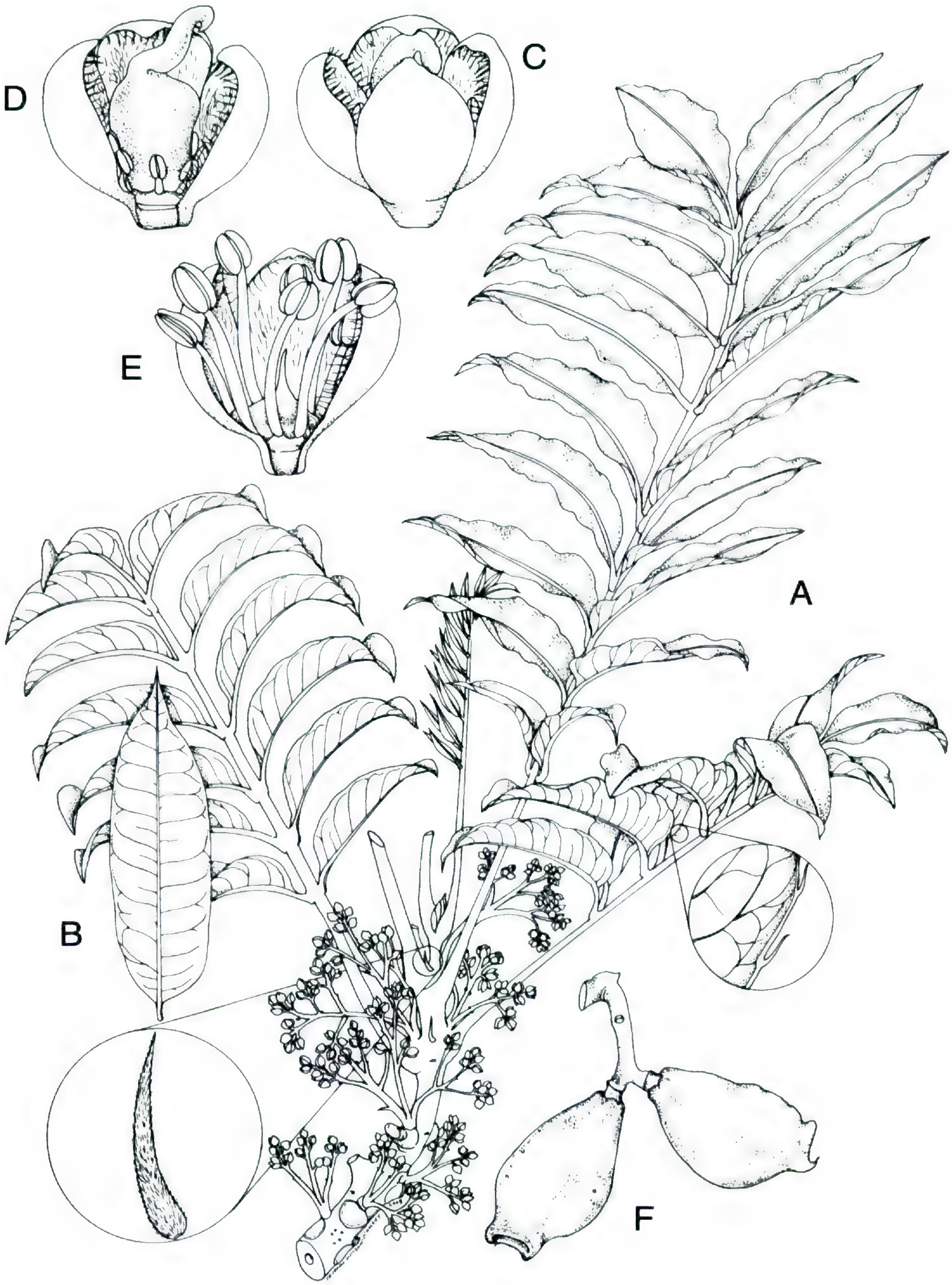

Figure 1. *Hooglandia ignambiensis* McPherson & Lowry. —A. Flowering twig of female material. —B. Abaxial view of a lateral leaflet. —C. Young female flower. —D. Female flower at anthesis, one sepal removed. —E. Male flower at anthesis, one sepal removed. —F. Fruit. (A, B, C, D, and F based on *Lowry et al. 5767,* MO; E based on *Lowry et al. 5770,* MO.)

6–7 mm wide; internodes hollow. *Leaves* imparipinnately compound, opposite, decussate, 26–37 cm long at maturity; leaflets (11 to)17 to 19, opposite, dark green and shiny above, paler beneath, chartaceous, oblong to weakly obovate, (5.5–)6–10.8 × (2–)2.5–3.3 cm, the lower 1(or 2) pairs smaller and often elliptic, occasionally caducous; blade glabrous at maturity except for sparse, short, subappressed hairs on the midvein beneath, the immature leaves sparsely short-subappressed pubescent on both surfaces, more densely so along the midrib; base obtuse, oblique in the lateral leaflets, margins minutely thickened beneath, entire or occasionally with 1 to 3(to rarely 7) very slender, fragile teeth per side, these usually terminating secondary veinlets in the basal third of the blade, or sometimes located instead near the apex, each tooth up to 1 mm long, the slender portion caducous and sometimes leaving behind a small, mucronate remnant; apex acuminate, tapering to a short mucro ca. 1 mm long, venation brochidodromous or semicraspedodromous with 11 to 14(to 16) pairs of opposite to subopposite secondary veins; domatia absent; petiolules 4–6 mm long, tinged reddish purple (in fresh material), short-subappressed pubescent, channeled above; rachis tinged reddish purple, with moderate to dense short, subappressed hairs; petioles 6.5–9.5 cm long, 2–3.5 mm diam., expanded somewhat at the base, flattened in dry material; stipels absent; stipules interpetiolar, linear, subterete, 8–10 mm long, occasionally divided nearly to the base or the two halves completely free from one another and separated by up to 3 mm, densely short-subappressed pubescent, caducous, leaving a small oblate scar ca. 1.5–3 mm wide; colleters absent. *Inflorescences* axillary, flowering sub-synchronous, the terminal flowers opening only slightly before the more basal ones, paniculate, short-subappressed pubescent throughout, borne in the axils of the upper 3 to 7 pairs of leaves, the short basal peduncle (0–)1–5(–6) mm long and bearing 3 ascending to recurved primary axes (1–)1.5–4.5 cm long in female plants, to 8 cm long in male plants, secondary axes (1)2 to 6, subopposite, the lowermost sometimes abortive and leaving an evident scar, each subtended by a caducous, narrowly triangular bract ca. 1.5–4 mm long, terminating in a 4- to 6-flowered cymule, the lowermost secondary axes also bearing 1 or 2 lateral cymules (tertiary axes), flowers subtended by a straight, spreading, narrowly triangular bracteole ca. 0.8–2 mm long, caducous prior to anthesis, leaving an evident scar; pedicels 0.3–1.5 mm long, jointed at or below the midpoint, the proximal portion pubescent, the distal portion glabrous. *Male flowers*: sepals 4, distinct, white, imbricate in bud, 2.5–3.5 mm long, 2.5–3 mm wide, rather thick, spreading at anthesis, glabrous abaxially, villose adaxially, ciliate; petals absent; stamens 8(–9), subequal, 4 mm long at anthesis and slightly exserted beyond the sepals; filaments 3 mm long, somewhat flattened; anthers 1 mm long, polleniferous, dorsifixed above the basal lobes, versatile, bilocular, dehiscence longitudinal and latrorse; pollen spheroidal, 13–16 μm diam., tricolporate, surface visibly psilate, slightly irregular; disk intrastaminal, adnate to base of the pistillode, annular, ca. 1.5 mm diam., slightly lobed around the bases of the filaments; pistillode conical, ca. 1.5 mm high including the erect style/stigma (1 mm long); locule and ovules vestigial; stigmatic portion of style/stigma minute, apparently unreceptive. *Female flowers*: sepals 4(5), distinct, white, in bud the 2 outer imbricate over the 2 inner, 2.5–3 mm long, 2.5–3 mm wide, rather thick, somewhat spreading, glabrous abaxially, villose adaxially, ciliate; petals absent; staminodes 8(–9), 1–1.5 mm long at anthesis, anthers 0.5–0.75 mm long, not or only slightly polleniferous, the pollen grains few, of various sizes, rarely containing cytoplasm; disk intrastaminodial, adnate to the base of the ovary, annular, lobed (sometimes deeply so) around the bases of the staminodes; gynoecium bilaterally symmetrical (excepting the bent style); ovary superior, green, somewhat flattened, 1 mm long, 1 mm wide on the wider face, roughly square in outline, glabrous, unilocular, the style/stigma arising from one distal corner and a faintly bilobed hump occupying the other distal corner, ovules 2, apical, anatropous, both attached at one end of an elongate, shallow trough, micropyle epitropous; style/stigma white, ca. 1 mm long, linear but crooked, not held erect, typically basally appressed to top of ovary and bent about mid-length through 90–180 degrees, the apparently stigmatic portion elongate. *Infructescences* borne in axils of the 2 or 3 pairs of leaves or leaf scars just below the inflorescences, each with 1 to 3 primary axes 3.6–6 cm long and bearing one or two fruit; fruit drupaceous, light green (in nearly mature fresh material), asymmetrically obovate to elliptic in outline, flattened and thus bilaterally symmetrical overall, 3.8–4.2 cm long, 2–2.2 cm wide, 0.5 cm thick, with a narrowly acute, slightly beaked apex ca. 3 mm long and a rounded distal boss ca. 5–6 mm diam., exocarp fleshy, endocarp hard; seed one, the other ovule aborting; testa thin; endosperm starchy, the grains spheroidal, (5–)7(–9) μm diam., oil not detected; radicle straight, ca. 5 mm long; cotyledons flat, green, ca. 18 mm long, ca. 11 mm wide.

Paratypes. NEW CALEDONIA. **Province Nord:** Mt. Ignambi, SW of Tchambouenne, 20°27′35″S, 164°35′41″E, 1150 m, 4 May 2002, *P. P. Lowry II, G. McPherson, T. Le Borgne & R. Pouytiela 5770* (CANB, G, MO, NOU, P).

Although the new species is here interpreted as unicarpellate, and thus unique within the family in this feature, a remnant of a second carpel may be present in the form of the astylous hump visible in both the female flower and the fruit (Fig. 1). However, dissections of the ovary revealed no further evidence that more than one carpel is involved. It may also be worth noting that, although Cronquist (1981) stated that the endosperm in the family is oily or absent, Dickison (1984), Takhtajan (1997), Fortune Hopkins and Hoogland (2002), and Bradford et al. (2004) describe it as starchy, as it is in *Hooglandia.*

Hooglandia ignambiensis is known only from dense, primary rain forest on the upper slopes of Mt. Ignambi in northeastern New Caledonia. The area is part of the Mt. Panié massif, which extends ca. 50 km from north of Mt. Mandjélia southeast to Mt. Panié. The massif has one of the most humid climates in New Caledonia, with recorded annual precipitation levels reaching 4000 mm (Section d'Hydrologie de l'ORSTOM & Service Territorial de la Météorologie, 1981), although rainfall on the upper slopes is certainly even higher (Lowry, 1998). The Mt. Panié massif is characterized by the presence of micaschist and related metamorphic rock types, in contrast to adjacent areas, which are largely dominated by soils derived from other substrates, including the distinctive ultramafic rocks that cover large portions of New Caledonia (Paris, 1981).

The Mt. Panié massif is a center of local endemism, with numerous species recorded only from the comparatively well-collected eastern side of Mt. Panié, and many others restricted to one or a few localities in northeastern New Caledonia. The palm flora of the area is particularly diverse, with 10 species endemic to the massif (Hodel & Pintaud, 1998). This led Pintaud et al. (2001) to recognize the Mt. Panié massif as one of five phytogeographic regions within New Caledonia based on the distribution of palm species. Few plant taxa appear to have been previously known only from Mt. Ignambi, but an endemic new species of gecko was recently described from the peak (Bauer et al., 2000).

Conservation status. Using the data available and applying the IUCN Red Data criteria (IUCN, 2001), we assign *Hooglandia ignambiensis* a provisional threat status of Critically Endangered (CR D) because only two mature individuals are known to exist. The area in which the plant grows, however, does not appear to be under any immediate threat. The single known population occurs well within a sizeable area of pristine forest, where it is protected from the fires that frequently burn in the surrounding secondary grasslands. Although local inhabitants occasionally hunt in the area, we saw no signs suggesting they exploit forest products, and other than the presence of a trail, a long-abandoned road, and a very small clearing on the summit, there was little evidence of human disturbance within the forested area.

A PDF version of this paper, including color images of *Hooglandia ignambiensis*, is available at: http://www.mobot.org/MOBOT/Research/newcaledonia/hooglandia.pdf.

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PHYLOGENETIC POSITION OF THE NEW CALEDONIAN ENDEMIC GENUS *HOOGLANDIA* (CUNONIACEAE) AS DETERMINED BY MAXIMUM PARSIMONY ANALYSIS OF CHLOROPLAST DNA[1]

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Abstract

To determine the phylogenetic position of a newly discovered New Caledonian genus, *Hooglandia* McPherson & Lowry, maximum parsimony analyses were performed using molecular sequence data from *Hooglandia* and existing *rbc*L and *trn*L-F data sets. An initial analysis using an *rbc*L data set with a broad sampling of flowering plants strongly suggested a position for *Hooglandia* within Cunoniaceae, a relationship further confirmed by analyses of *rbc*L and *trn*L-F chloroplast data sets using a more focused sample of taxa from Oxalidales. The position of *Hooglandia* in Cunoniaceae is supported by its possessing interpetiolar stipules and starchy endosperm. This paper provides a rare example whereby molecular data were used to guide the familial placement of a newly discovered plant genus concomitant with its description.

Key words: Cunoniaceae, DNA taxonomy, *Hooglandia*, molecular systematics, New Caledonia.

In a companion paper, McPherson and Lowry (2004, this issue) describe *Hooglandia* as a new genus of Cunoniaceae from Mt. Ignambi in northeastern New Caledonia. When material of this new taxon was first collected, it clearly represented a new species and was regarded as possibly the first material of a new genus or family. However, determining the affinities of the new plant proved problematic, as it had morphological features common to members of both Oxalidales and Sapindales but did not have a combination of features characteristic of any of the families or genera within these orders (McPherson & Lowry, 2004). To aid in the taxonomic placement of *Hooglandia*, the first author conducted molecular phylogenetic analyses to investigate the phylogenetic position of the newly discovered taxon. While the impacts of molecular phylogenetic techniques on plant systematics have been substantial (e.g., Chase et al., 2000; Crawford, 2000; Stevens, 2000), their integrated use in the placement of newly discovered taxa has not been a common practice among plant systematists (but see Garnock-Jones et al., 1996). Here we present the results of a nested series of molecular phylogenetic analyses using sequence data from two chloroplast regions (*rbc*L and *trn*L-F) that proved essential for determining the relationship of *Hooglandia* and assessing its placement among the currently recognized flowering plant families (McPherson & Lowry, 2004).

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Materials and Methods

Choice of Markers

Two molecular markers from the chloroplast genome (*rbc*L and *trn*L-F) were selected for the phylogenetic analysis of *Hooglandia*. They were chosen for three main reasons: (1) many sequences from these regions were readily available in internet databases; (2) their taxonomic representation was broad; and (3) the level of sequence variation seemed appropriate for assessing the phylogenetic placement of the new entity at the ordinal and familial levels. An initial analysis was performed to place *Hooglandia* within the angiosperms using the *rbc*L data set of Chase et al. (1993), which has proven useful in resolving relationships among the major groups of flowering plants. Once the first analysis indicated that *Hooglandia* was related to members of Oxalidales (sensu APG, 2003), and in particular to Cunoniaceae, the *trn*L-F and *rbc*L data sets of Bradford and Barnes (2001) were then used to evaluate the likely position of *Hooglandia* within the order. The Bradford and Barnes (2001) data sets included representative genera from across Oxalidales as well as a nearly comprehensive sampling of genera from Cunoniaceae. All of the data sets utilized in the present study are available in TreeBASE (TreeBASE © 1994–2003, www.treebase.org).

DNA Sequencing

Total genomic DNA was extracted from approximately 2 grams of leaf material of *Hooglandia ignambiensis* McPherson & Lowry that was collected in the field and preserved in a 2X CTAB salt-saturated solution (Rogstad, 1992). Extractions were performed using the modified CTAB method of Doyle and Doyle (1987) and were further purified in cesium chloride/ethidium bromide gradients via ultracentrifugation. The herbarium voucher for the extracted DNA is *P. P. Lowry II, G. McPherson, T. Le Borgne & R. Pouytiela 5767* (MO), the type of *H. ignambiensis* from New Caledonia.

The *rbc*L gene was amplified in one fragment using forward primer Z1 (Wolf et al., 1994) and reverse primer 1460R (G. Zurawski, unpublished). The resulting product was sequenced using the above primers as well as primers 427F, 997F, 515R, and 1081R (Goffinet et al., 1998). The PCR reaction conditions used to amplify *rbc*L were 97°C (4 min.); then 39 cycles of 94°C (30 sec.), 53°C (1 min.), 68°C (2 min.); followed by 72°C (7 min.). The *trn*L-F region amplified with the forward primer C and reverse primer F of Taberlet et al. (1991) and was sequenced using their forward primers C & E and reverse primers D & F. The PCR reaction conditions used to amplify *trn*L-F were 97°C (4 min.); then 39 cycles of 94°C (30 sec.), 48°C (1 min.), 72°C (1.5 min.); followed by 72°C (7 min.). All resulting PCR products were purified using the Qiaquick PCR purification kit (Qiagen, Valencia, California, U.S.A.). PCR products were fluorescence-labeled according to the manufacturer's protocol using "Big-Dye" (Applied Biosystems) cycle sequencing and were sequenced on an ABI version 377 automated sequencer.

The resulting sequences were proofed and edited, and double stranded contigs were assembled using Seqman 4.0 (DNAStar). Preliminary alignments were constructed using ClustalX (Thompson et al., 1997) and then adjusted manually in MacClade 4.05 (Maddison & Maddison, 2002). Insertions and deletions (indels) shared by two or more taxa and greater than one bp in length were coded and added to the data sets as additional binary characters. All sequences generated in this study were deposited in GenBank and have accession numbers AY549639 (*trn*L, *trn*L intron), AY549640 (*trn*L-F spacer), and AY549641 (*rbc*L).

Phylogenetic Analysis

Global rbc*L analyses*

To determine the phylogenetic position of *Hooglandia* among the angiosperms, its *rbc*L sequence data were aligned to the 500-taxon *rbc*L data set of Chase et al. (1993) (downloaded from Ken Rice's Treezilla web site, http://www.cis.upenn.edu/~krice/treezilla/) and analyzed using maximum parsimony (MP) analysis. Because of the large size of the matrix (501 taxa, 1428 characters), the Parsimony Ratchet (Nixon, 1999) was implemented in PAUP* version 4.0b10 (Swofford, 2002) using the setup and batch files generated in PAUPRat (Sikes & Lewis, 2001). Fifteen ratchet runs of 200 iterations each were conducted, with 15% of the characters perturbed per iteration and equal starting weights. The number of perturbed characters was chosen after running preliminary Ratchet searches with different numbers of perturbed characters (Sikes & Lewis, 2001). All of the shortest, unperturbed trees from each iteration were brought into PAUP using the GET TREES FROM FILE option and filtered to keep only those of shortest length, which were then used to generate a consensus tree. To obtain an estimate of support for individual branches, 1000 bootstrap (BS) replicates were run [with TBR branch swapping, MULTREES option off, COLLAPSE option on, STEEPEST DESCENT option

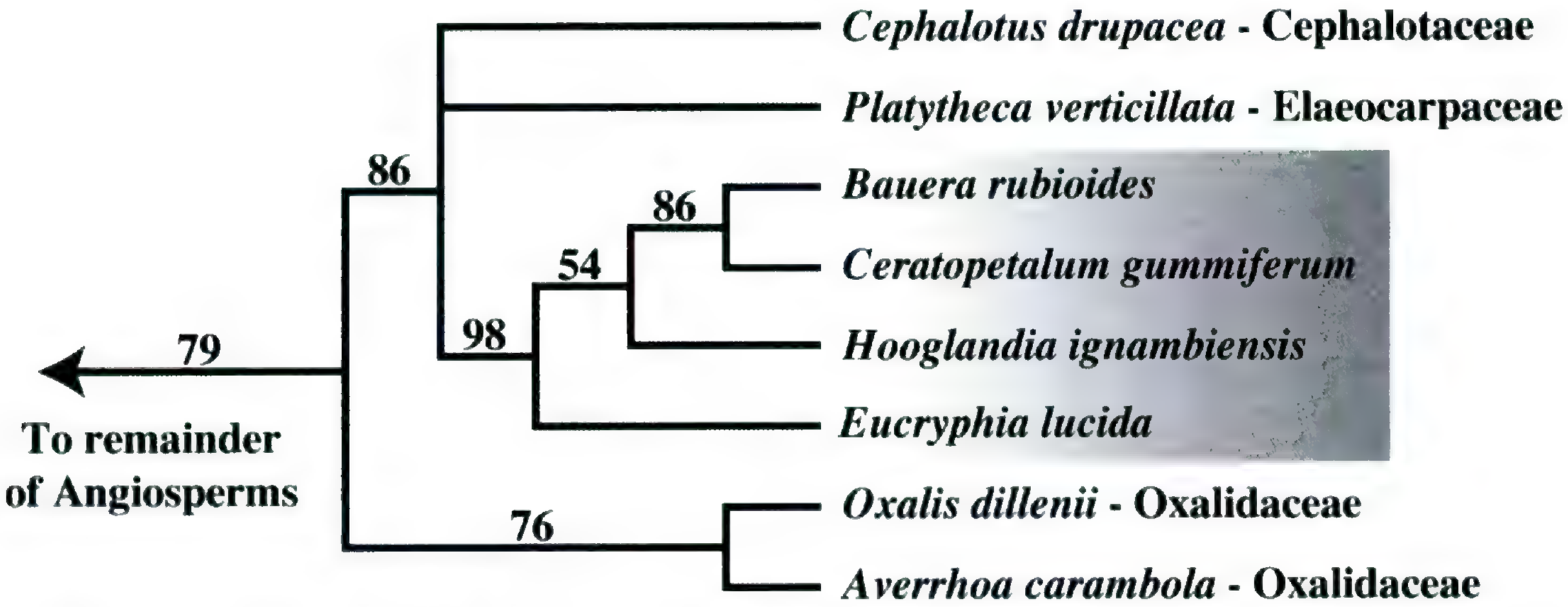

Figure 1. A portion of the 50% bootstrap consensus tree produced by 1000 resampling replicates of the 501-taxon *rbc*L data set (sensu Chase et al., 1993). Significant bootstrap percentage values are shown above the branches. The shaded box surrounds members of Cunoniaceae. Other family assignments are indicated (sensu APG, 2003).

off, and gaps treated as missing data]. Simulation studies by DeBry and Olmstead (2000) indicated that BS analyses using TBR branch swapping with the MULTREES option set to *off* produce values "essentially identical" to those in which the MULTREES option is *on* while requiring less time to run.

Focused rbc*L and* trn*L-F analyses*

After the approximate position of *Hooglandia* was determined to lie among Oxalidales, *rbc*L and *trn*L-F data were aligned to the data sets of Bradford and Barnes (2001), which these authors had used to evaluate relationships among the genera of Cunoniaceae and which included several genera from other families in Oxalidales as outgroups. We used their data sets A (*rbc*L), B (*trn*L-F), and C (*rbc*L and *trn*L-F), downloaded from TreeBASE (© 1994–2003, www.treebase.org), for the MP analyses. For the *rbc*L and combined analyses, characters were unweighted and unordered, and 1000 heuristic search replicates were performed in PAUP* version 4.0b10 [same options as before but with the default setting of MULTREES option on]. Strength of support for individual branches was again assessed using 1000 bootstrap replications (Felsenstein, 1985). Because of time and computer memory constraints, the *trn*L-F data set was analyzed using the Parsimony Ratchet, which was implemented as described above for the analysis of the 501-taxon *rbc*L data set. To determine if the *rbc*L and *trn*L-F data sets were combinable, Shimodaira-Hasegawa tests (Goldman et al., 2000; Doust & Drinnan, 2004) were implemented in PAUP*, with RELL optimization and 1000 replicates.

Results

Global *rbc*L analysis

Alignment of the 501-taxon data set, that is, the sequences for 500 taxa used by Chase et al. (1993) plus the sequence data from *Hooglandia*, resulted in a data set with a total length of 1428 base positions; 798 characters were parsimony informative. The Parsimony Ratchet resulted in 60 unique, shortest length trees of 16,650 steps each (Consistency Index (CI) excluding uninformative characters = 0.1017; Retention Index (RI) = 0.6390). The strict consensus tree produced by the Parsimony Ratchet places *Hooglandia* among a group of genera belonging to Oxalidales. Figure 1 shows the Oxalidales clade that resulted from MP analysis of the 501-taxon *rbc*L data set. *Hooglandia* is strongly supported (BS = 98%) as part of a clade containing three sampled members of Cunoniaceae. Table 1 provides the authorities for the taxa in Figure 1.

Focused *rbc*L and *trn*L-F analyses

rbc*L analysis*

The aligned *rbc*L data set, representing 38 taxa, contained sequences with a total length of 1477 bp. Maximum parsimony analysis resulted in three trees of 447 steps (CI excluding uninformative characters = 0.5222; RI = 0.6774); 121 characters were parsimony informative. The topology of the strict consensus tree (not shown) was congruent with the *rbc*L tree found by Bradford and Barnes (2001) using their data set A (see their fig. 1), differing in the inclusion of *Hooglandia*. This newly described genus (see McPherson & Lowry, 2004)

Table 1. Authorities for taxa used in the global *rbc*L and focused *rbc*L and *trn*L-F phylogenetic analyses.

Outgroup taxa
Aristotelia chilensis Stuntz
Averrhoa carambola L.
Brunellia colombiana Cuatrec.
Brunellia oliverii Britton
Cephalotus drupacea Siebold & Zucc.
Cephalotus follicularis Labill.
Crinodendron patagua Molina
Elaeocarpus reticulatus Ridl.
Eucryphia lucida Druce
Oxalis dillenii Jacq.
Platytheca verticillata Baill.

Ingroup taxa (Cunoniaceae sensu Bradford & Barnes, 2001)
Ackama paniculosa Beuzev. & C. T. White
Acrophyllum australe (A. Cunn.) Hoogland
Acsmithia elliptica (Vieill. ex Pamp.) Hoogland
Anodopetalum biglandulosum (Hook.) Hook.f.
Bauera rubioides Andrews
Caldcluvia paniculata D. Don
Callicoma serratifolia Andrews
Ceratopetalum gummiferum Small
Codia discolor (Brongn. & Gris) Guillaumin
Cunonia atrorubens Schltr.
Davidsonia pruriens F. Muell.
Eucryphia cordifolia Cav.
Geissois benthamii F. Muell.
Gillbeea adenopetala F. Muell.
Hooglandia ignambiensis McPherson & Lowry
Pancheria engleriana Schltr.
Platylophus trifoliatus D. Don
Pseudoweinmannia lachnocarpa (F. Muell.) Engl.
Pullea glabra Schltr.
Spiraeopsis celebica Miq.
Spiraeanthemum samoense A. Gray
Weinmannia bangii Rusby
Weinmannia madagascariensis DC. ex Ser.
Weinmannia raiateensis J. W. Moore
Vesselowska rubifolia (F. Muell.) Pamp.

was placed in a subbasal clade of Cunoniaceae with strong support (BS = 100%).

trn*L-F analysis*

The total length of the aligned sequences in the *trn*L-F data set was 1282 bp. To decrease computing time, Cunoniaceae taxa included in the *trn*L-F data set of Bradford and Barnes (2001) (data set B) but absent from their *rbc*L data set were excluded, resulting in a reduced sample of 36 taxa. The excluded taxa were all from well-supported genera that had multiple representatives in the original data set. Alignment of the *trn*L-F sequences required 95 indels, of which only 27 were parsimony informative and greater than 2 bp in length. The 27 parsimony-informative indels were coded as binary characters and appended to the end of the molecular data set. *Hooglandia* did not have either the "Big" or "Small" deletions as identified by Bradford and Barnes (2001) for *trn*L-F. The Parsimony Ratchet resulted in 2996 shortest-length trees. The bootstrap consensus tree (not shown) resulting from the analysis of the *trn*L-F data was visually congruent with the consensus tree resulting from the analysis of data set B in Bradford and Barnes (see their fig. 2, 2001), differing notably by the exclusion of certain taxa (as mentioned above) and the inclusion of *Hooglandia*, which was again placed within a subbasal clade of Cunoniaceae (BS = 100%).

Combined rbc*L* + trn*L-F analysis*

Shimodaira-Hasegawa (SH) tests (Goldman et al., 2000) were employed to determine if significant differences existed in the topologies produced by the *rbc*L and *trn*L-F data sets (e.g., Doust & Drinnan, 2004). To test for effects of differing topologies within a data set, trees from an unconstrained analysis were compared to trees constrained by either of the topologies derived from the other data set and the combined data set. Specifically, the topology produced by an unconstrained analysis of the *rbc*L partition was compared against the 70% bootstrap consensus trees produced by MP analysis of the *trn*L-F data set and by analysis of the combined *rbc*L/*trn*L-F data set. The reciprocal comparison was performed on an unconstrained *trn*L-F topology tested against the 70% bootstrap consensus trees produced by MP analysis of the *rbc*L data set and by analysis of the combined *rbc*L/*trn*L-F data set. In all such tests no significant differences were found ($P > 0.05$), indicating that there is no conflict between the phylogenetic signal derived from each data set. The SH tests thus indicated that the data sets could be combined for further analysis.

The length of the sequences in the combined *rbc*L/*trn*L-F data set was 2695 bp. Maximum parsimony analysis resulted in 15 trees of 770 steps: 222 characters were parsimony informative (CI excluding uninformative characters = 0.6009; RI = 0.7014). One of the shortest-length trees is shown in Figure 2, with branch lengths indicated. Figure 3 shows the topology of the 50% strict consensus of the bootstrap analysis (see legend). The strongly supported branches (BS > 70%) are the same as those produced by analysis of data set C of Bradford and Barnes (see their fig. 3, 2001). Again, *Hooglandia* was placed in a subbasal clade of Cunoniaceae with strong support (BS = 100%). Table 1 provides the authorities for the taxa in Figures 2 and 3.

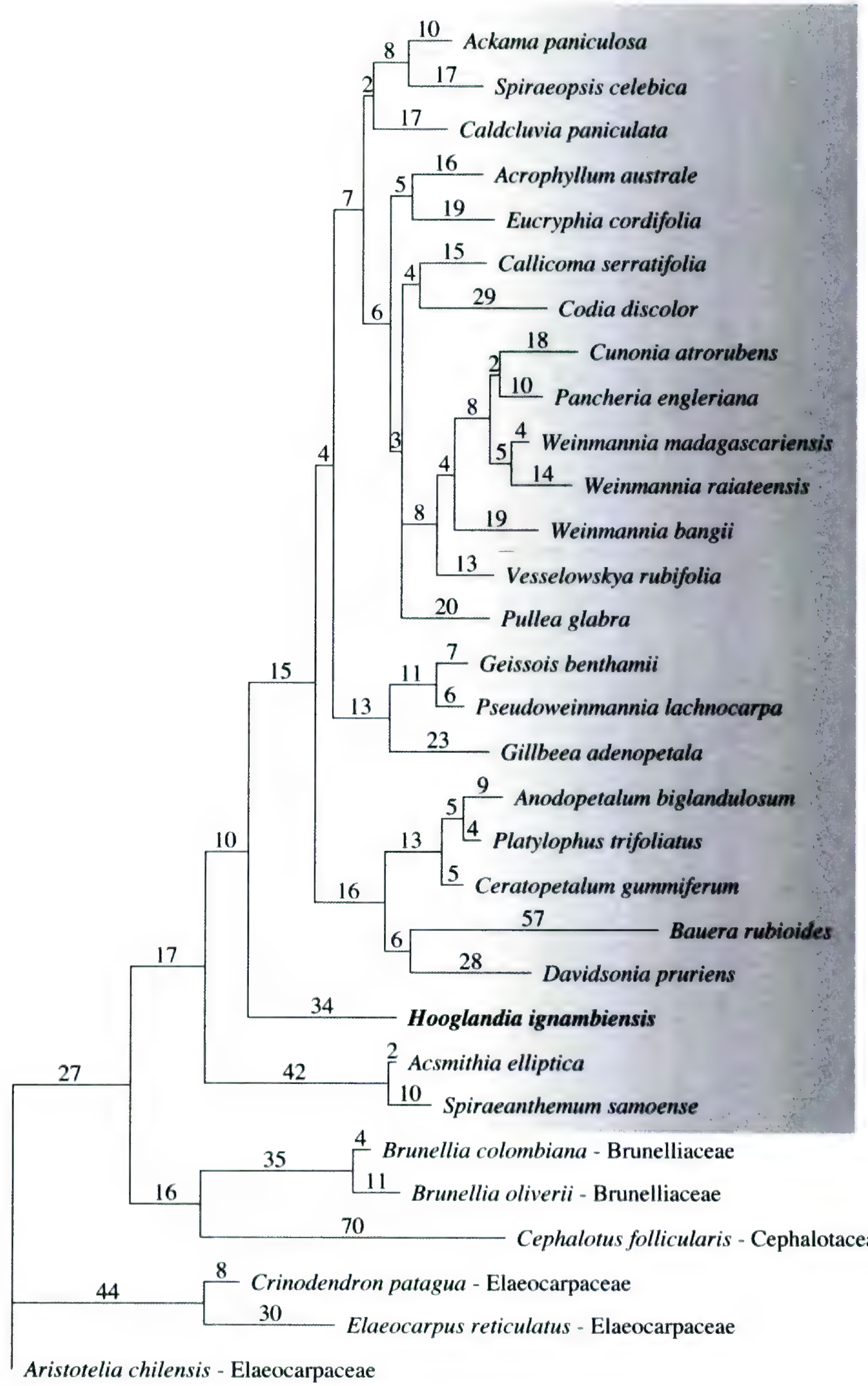

Figure 2. One of 15 minimum-length trees of 770 steps produced by maximum parsimony analysis of the combined *rbc*L/*trn*L-F data set. Branch lengths are shown above the branches. The shaded box surrounds members of Cunoniaceae, as circumscribed by Bradford and Barnes (2001). Other family assignments are indicated (sensu APG, 2003).

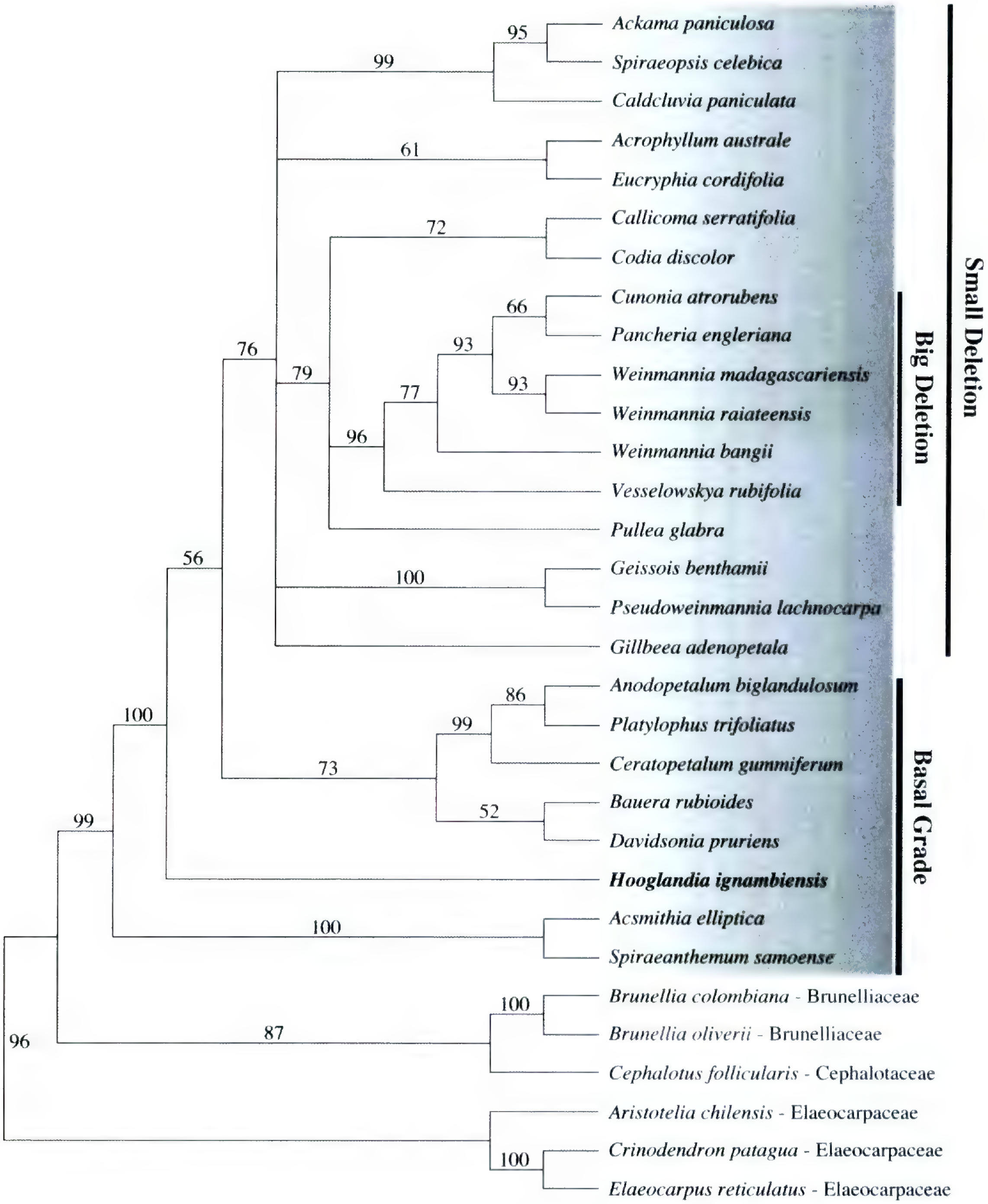

Figure 3. The 50% bootstrap consensus tree produced by 1000 resampling replicates of the combined *rbc*L/*trn*L-F data set. Numbers above branches represent bootstrap percentage values. The shaded box surrounds members of Cunoniaceae, as circumscribed by Bradford and Barnes (2001). Taxa possessing the "Small" and "Big" deletions (*trn*L-F) and the Basal Grade of Bradford and Barnes (2001) are indicated. Other family assignments are indicated (sensu APG, 2003).

While *Hooglandia* is clearly a member of Cunoniaceae, its exact position within the family is, however, equivocal. In both the MP and 50% bootstrap consensus (Figs. 2, 3) trees for the combined data, *Hooglandia* is placed in a large clade that is sister to the basal-most clade (comprised of *Acsmithia* and *Spiraeanthemum*) in the family. *Hooglandia* is then sister to the remaining members of the

family, although this relationship is weakly supported (Fig. 3, BS = 56%). If this branch is collapsed, the position of *Hooglandia* is unresolved within the Basal Grade sensu Bradford and Barnes (see their fig. 2, 2001: 361, and Fig. 3 herein).

Discussion

Phylogenetic position of *Hooglandia*

The primary goal of the molecular phylogenetic analyses presented in this paper is to establish the placement of a newly discovered plant from New Caledonia, described by McPherson and Lowry (2004) as *Hooglandia ignambiensis*. The results obtained from the analysis of *rbc*L and *trn*L-F sequence data strongly support the inclusion of *Hooglandia* within Cunoniaceae. *Hooglandia* falls above the first-branching clade within the family, comprised of *Acsmithia* Hoogland and *Spiraeanthemum* A. Gray, well within the bounds of the family as circumscribed by Bradford and Barnes (2001).

Hooglandia possesses interpetiolar stipules, which may represent the only clear synapomorphy for Cunoniaceae. Bradford and Barnes (2001: 370) described most basal Cunoniaceae as having brachyparacytic subsidiary cells in the leaf epidermis and suggest that this condition may also be a synapomorphy for the family. Unlike other basal Cunoniaceae, *Hooglandia* has what are best described as anomocytic subsidiary cells, although they do not fit neatly into any described stomatal type (sensu Metcalf & Chalk, 1974). Epidermal peels from the abaxial surface of the middle of two leaflets of the type specimen of *H. ignambiensis* were examined during the course of this investigation. The guard cells (average length of 12.2 μm, cell number or N = 20, standard deviation or s.d. = 0.92) are slightly everted and partly overlie the surrounding 4 to 7 (N = 20, average = 5.25, s.d. = 0.75) polygonal subsidiary cells, which are similar in shape to the surrounding epidermal cells, differing only in their smaller size (average length of 8.65 μm (N = 20, s.d. = 1.93) vs. 12.73 μm (N = 20, s.d. = 3.1) and average width of 6.65 μm (N = 20, s.d. = 1.87) vs. 9.58 μm (N = 20, s.d. = 2.29)). There seems to be some discrepancy in the scoring of subsidiary cell arrangement in Cunoniaceae, as Dickinson (1975) classified the stomatal type for many genera differently than Bradford and Barnes (2001). This disagreement suggests that there may be variation in stomatal types within species and genera of Cunoniaceae and that caution should be exercised when using stomatal type as a systematic character within the family.

Another feature supporting the placement of *Hooglandia* in Cunoniaceae is its possession of starchy endosperm, a feature shared among all members of the family but absent in the mature ovules of most other members of Oxalidales (except Oxalidaceae and *Brunellia* Ruiz & Pav.) and unusual within Rosids (sensu APG, 2003). Starchy endosperm is not present in Sapindales, one of the groups to which it was initially thought that *Hooglandia* might belong.

Other characters that support the inclusion of *Hooglandia* in Cunoniaceae (but do not necessarily represent synapomorphies for the family) include opposite imparipinnately compound leaves, paniculate inflorescences, tetramerous flowers, a diplostemonous androecium, an intrastaminal disk, and a superior bi-ovulate ovary.

Evolutionary implications

Because the sister relationship of *Hooglandia* to the remainder of the genera within Cunoniaceae (except for the basally branching clade comprising *Acsmithia* + *Spiraeanthemum*) is only weakly supported, it would be premature to base any interpretations of character evolution on the topology revealed by the present analyses (Figs. 2, 3). Nevertheless, the position of *Hooglandia* among basal Cunoniaceae is supported by its possessing tricolporate pollen, secondary veins terminating teeth on the leaflets, and the presence of anthers with a thecal connective protuberance (see fig. 5 in Bradford & Barnes, 2001).

Specialists working on Cunoniaceae agree that *Hooglandia* resembles *Aistopetalum* and that it might therefore be closely related to it (Barnes & Hopkins, pers. comm.). A sister relationship between *Hooglandia* and *Aistopetalum* is also weakly supported by cladistic analysis of morphological data (Bradford & Sweeney, unpublished data). In these morphological analyses, *Hooglandia* and *Aistopetalum* are sister to *Davidsonia* F. Muell., and these three taxa form a clade occupying a subbasal position between a clade containing *Acsmithia* and *Spiraeanthemum* and its sister clade comprising the rest of the family. Characters supporting a close relationship between *Aistopetalum*, *Hooglandia*, and *Davidsonia* include imparipinnate leaves, paniculate inflorescences, and indehiscent drupaceous fruits. Unfortunately, extraction of DNA from herbarium specimens of *Aistopetalum* has so far failed. Relationships among the Basal Grade of Cunoniaceae (see fig. 2 in Bradford & Barnes, 2001; Fig. 3 herein) are poorly understood, and this situation draws attention to *Aistopetalum* as a priority

genus for further molecular systematic investigation.

Hooglandia is dioecious, as are species of *Pancheria* Brongn. & Gris, *Vesselowskya* Pamp., and *Weinmannia* L., which belong to a derived clade within Cunoniaceae (Figs. 2, 3). The position of *Hooglandia* relative to the clade containing *Pancheria, Vesselowskya,* and *Weinmannia* would suggest that dioecy arose in parallel in these two clades.

Hooglandia is unique within Cunoniaceae and Oxalidales in its possessing a unicarpellate (or perhaps pseudomonomerous) ovary versus 2(3–14)-carpellate ovaries in the rest of the family and order (McPherson & Lowry, 2004). It is also unique within the family in its possessing bilaterally symmetrical, drupaceous fruits.

THE ROLE OF MOLECULAR DATA IN DESCRIPTIVE SYSTEMATICS

Several recent advances have had tremendous impact on the field of plant systematics, including the increased ease of obtaining DNA sequence data, improvements in computer technology, and the development of more powerful phylogenetic software (Chase et al., 2000; Crawford, 2000; Stevens, 2000). While these changes have provided important new insights into the evolutionary relationships among organisms and have prompted significant modifications to modern classification systems of flowering plants, molecular techniques have been used only sparingly by plant systematists when describing new taxa. This is not surprising, as the taxonomic group to which most newly discovered plants belong is often readily and accurately inferred from its phenotype. However, some authors have raised the point that taxonomic expertise is unfortunately vanishing and that molecular data may have to play a more substantial role in descriptive systematics (Godfray, 2002; Hebert et al., 2003; Tautz et al., 2003). Molecular data have already been used to identify and describe entities in groups that present a limited number of phenotypic characters or in which features are ambiguous or hard to interpret, such as nematodes (Floyd et al., 2002), bacteria (Jonasson et al., 2002), and fungi (Redecker et al., 1997). In what was touted as one of the first examples of such an application of molecular data in flowering plants, Garnock-Jones et al. (1996) assessed the family-level placement of an unknown sterile plant collected in New Zealand, concluding that it could be an unnamed new genus of Cunoniaceae or a dwarf mutant of *Weinmannia racemosa* L. f. Subsequently, Bradford and Barnes's (2001) phylogenetic analyses suggested that the particular accession examined by Garnock-Jones et al. (1996) may indeed belong to *W. racemosa.* Although it is uncommon among flowering plants to encounter cases where the relationships of an organism are uncertain, when they do arise, molecular techniques offer an ideal way to evaluate relationships quickly and efficiently. In the case of *Hooglandia,* it took some 12–15 hours to extract, amplify, sequence, and analyze the *rbc*L and *trn*L-F data sets. By contrast, it was not possible using morphology to place *Hooglandia* with confidence even at the ordinal level. In this case, molecular data proved to be indispensable for recognizing that *Hooglandia* is a member of Cunoniaceae.

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EVOLUTION OF VERONICEAE: A PHYLOGENETIC PERSPECTIVE[1]

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ABSTRACT

The genus *Veronica* (Plantaginaceae, formerly Scrophulariaceae) is well known for its reduced corolla tube in an otherwise long-tubed family. Similar character reversals to states thought to be plesiomorphic to taxa outside *Veronica* are found in inflorescence morphology, embryology, and karyology. We have used nuclear ribosomal ITS and plastid *trn*L-F sequence data in separate and combined data sets to explore character evolution in *Veronica* and related genera. We here use *Veronica* in a wide sense including the Hebe complex, *Synthyris*, *Besseya*, and *Pseudolysimachion*. Based on comparison with results from the molecular analyses, we infer the rosette habit to be ancestral in the tribe Veroniceae with two losses and at least two regains. The terminal inflorescence was probably lacking in the ancestor of Veroniceae but re-emerged at least twice with a concentration in annual and alpine species. Tubular flowers evolved in parallel several times, and this parallelism is also indicated by floral development. The ancestor of Veroniceae was likely to have five calyx lobes and four corolla lobes, but both characters are labile. The capsule of the ancestor of *Veronica* was probably wide and compressed with several specializations occurring within species groups. The pollen types identified by earlier authors match with little conflict results from the molecular analyses, as do embryological characters such as morphology of micropylar endosperm haustoria. Finally, chromosome number was likely to be $x = 9$ in the ancestor of Veroniceae with other base numbers evolving several times in parallel. Similarities of the inferred ancestral character states with those from the outgroups *Plantago* and *Digitalis* are discussed.

Key words: character evolution, ITS, molecular systematics, *trn*L-F, *Veronica*, Veroniceae.

The genus *Veronica* L. (Plantaginaceae sensu APG, 2003; formerly Scrophulariaceae) is characterized by its more or less short-tubed to subrotate and subactinomorphic flower, whereas most of its relatives in Lamiales (sensu APG, 2003) have long-tubed zygomorphic flowers. *Veronica* is an example of a taxon with generally derived characters in which many species developed character states otherwise considered plesiomorphic. These character reversals are not only found in the flower but also in inflorescence morphology, embryology, and karyology. The following reversals occur in at least some species: the corolla tube becomes reduced to an almost choripetalous state; a zygomorphic flower becomes almost actinomorphic; the thyrse becomes reduced to a raceme; corolla lobes become reduced from five to four by fusion of the adaxial lobes. The same can happen in the calyx. Stamen number becomes reduced from four to two. Endosperm haustoria become reduced from four uninucleate cells to one bi- or uninucleate cell. Such character transitions have drawn the interest of scientists for decades (e.g., Lehmann, 1918; Hamann, 1960; Kampny & Dengler, 1997). The differentiation between terminal and strictly lateral inflorescences and between annual and perennial life histories, for example, has been considered a major division in the genus (Römpp, 1928; Elenevskij, 1977). Molecular data now give the opportunity to evaluate previous hypotheses of character evolution in the tribe Veroniceae. We have already discussed some of these characters in previous publications (Albach & Chase, 2001; Albach et al., in press a; see also Martínez-Ortega & Rico, 2001) and shown the non-informativeness of the inflorescence and life history characters toward a taxonomic revision of the genus. We have therefore proposed a revised classification for *Veronica* (Albach et al., in press b) that includes the Hebe complex, *Synthyris*, *Besseya*, and *Pseudolysimachion*. In this circumscription, *Veronica* includes 13 subgenera. The Hebe complex is divided into two subgenera, the Australian species of *Veronica* and *Derwentia*, and the New Zealand core-Hebe group. *Synthyris* and *Bes-*

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seya are combined in subgenus *Synthyris*, while *Pseudolysimachion* is reduced to subgeneric rank. Subgenus *Veronica* includes many Eurasian and African montane to alpine species with a base chromosome number of $x = 9$, whereas those with $x = 8$ are found in subgenus *Stenocarpon*. Subgenus *Pentasepalae* includes most southwest Asian species along with European species from dry meadows. Subgenus *Beccabunga* includes the relatives of *V. beccabunga*, *V. serpyllifolia*, and the annual relatives of *V. acinifolia*. Subgenus *Chamaedrys* includes *V. chamaedrys* and relatives along with the annual *V. arvensis* and *V. verna*. Purely annual subgenera are subgenus *Cochlidiosperma* (*V. hederifolia*, *V. cymbalaria*, and relatives), subgenus *Pellidosperma* (*V. triphyllos* and relatives), subgenus *Triangulicapsula* (*V. grisebachii*), and subgenus *Pocilla* (*V. agrestis* and *V. biloba* with relatives). We will use *Veronica* in this wide sense in the following, although sometimes terming it *Veronica* s.l. for special emphasis of this wider circumscription. New molecular data for the nuclear ribosomal ITS and the plastid *trn*L-F regions for more taxa than in previous analyses (Albach & Chase, 2001; Albach et al., in press a), representing most of the diversity in the genus and related genera in Veroniceae, give here the opportunity to analyze character evolution in *Veronica* more thoroughly.

Materials and Methods

We have sampled 71 taxa of the Veroniceae representing most of the diversity in the tribe with the exception of species from the Southern Hemisphere (the Hebe complex), which represents a radiation of its own (species including authorities are listed in Table 1). Taxon sampling among subgenera is unequal, with taxon density ranging from 10 to 60% of the species to reflect infrasubgeneric diversity. An additional 11 taxa were included to represent taxa related to Veroniceae following results from previous analyses (Albach & Chase, 2001; Olmstead et al., 2001). *Oreosolen*, *Lafuentea*, and *Sibthorpia* have been used as outgroups. The analysis extends the sampling of the previous analysis of ITS (Albach & Chase, 2001) and *trn*L-F (Albach et al., in press a) with 43 new ITS sequences and 32 new *trn*L-F sequences. We present matching data sets with DNA from the same specimen for both regions with the exception of *Veronica glauca*, *V. abyssinica*, *Parahebe vanderwateri*, *Plantago lanceolata*, and *P. major* (vouchers listed in Table 1). Taxon sampling in the Hebe complex has been restricted because an evaluation of these species is presented elsewhere (e.g., Wagstaff et al., 2002). We have used the classification of Albach et al. (in press b) of *Veronica* including *Synthyris*, *Besseya* (both considered together as *Veronica* subg. *Synthyris*), and the Hebe complex (subgenera *Derwentia* and *Hebe*), although for species in the Hebe complex we retained their combination under their other genus name because new combinations have not been made for all species. Voucher specimens were made for all plants used in this study (Table 1).

DNA extraction, amplification, and sequencing

The protocol followed previous studies (Albach & Chase, 2001; Albach et al., in press a). Total genomic DNA was extracted from herbarium material and silica-gel-dried leaf samples according to the 2x CTAB procedure of Doyle and Doyle (1987) and then washed twice with 70% ethanol. DNA pellets were dried and resuspended in TE-buffer.

The *trn*L intron, 3′exon, and *trn*L-F spacer (hereafter *trn*L-F) were amplified with primers c and f of Taberlet et al. (1991). ITS sequences were amplified and sequenced using the primers 17SE (Sun et al., 1994) and ITS4 (White et al., 1991). In contrast to previous amplifications, we did not add DMSO, which facilitates amplification when there are problems with secondary structure, because we found it inhibits PCR when DNA quality was low. PCR products were run on a 1.0% TBE-agarose gel, cut out of the gel, and cleaned using QIAquick™ PCR purification and gel extraction kit (Qiagen GmbH, Hilden, Germany) following the manufacturer's protocols. Sequencing reactions (10 µl) were carried out using 1 µl of the Taq DyeDeoxy Terminator Cycle Sequencing mix (Applied Biosystems Inc.). Reactions were run out on a Prism 377 automated sequencer (Applied Biosystems Inc.), and both strands were sequenced. Sequences were assembled and edited using Sequence Navigator™ (Applied Biosystems Inc.). Assembled sequences were manually aligned prior to analysis. All sequences have been deposited in GenBank (accession numbers listed in Table 1). Aligned sequence matrices are available from DCA and MWC by request.

Sequence analysis

Insertions and deletions are frequent in both DNA regions (ITS and *trn*L-F). In a conservative approach we scored gaps as missing data, thus removing them from the analysis. The matrices were analyzed with PAUP* 4.0b7–10 (Swofford, 1998) using heuristic parsimony search methods. Both simple and random (with 10 replicates) taxon ad-

Table 1. Voucher specimens, sources, and GenBank accession numbers (or reference to where this information can be found) of ITS and *trn*L-F sequences used in this study. For partial sequences, the number of characters available is given in parentheses.

Species	ITS	*trn*L-F	Country. Locality	Voucher	ITS GENBANK	*trn*L-F GENBANK
			Veroniceae			
Lagotis angustibracteata P. C. Tsoong & H. P. Yang	+	+	China. Qinghai	*Miehe et al. 98-31710* (GOET)	Albach & Chase (2001)	Albach et al. (in press a)
Lagotis stolonifera (C. Koch) Maxim.	+	+	Caucasus. Cult. BG Bonn	*Albach s.n.* (WU)	AF509814	Albach et al. (in press a)
Paederota bonarota L.	+	+	Italy. Dolomites	*Albach 213* (WU)	AF509812	AF513353
Paederota lutea L.	+	+	Austria. Eisenkappler Hütte	*Albach 209* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
Parahebe vanderwateri (Wernham) Royen	+	−	New Guinea	*Buxton* (CHR 530002)	Wagstaff & Garnock-Jones (1998)	—
Parahebe vanderwateri (Wernham) Royen	−	+	New Guinea	*Barker 59* (K)	—	Albach et al. (in press a)
Picrorhiza kurrooa Royle	+	+	India. Cult. RBG Kew	*McBeath 2214* (K)	AF509813	Albach et al. (in press a)
Veronicastrum liukiuense (Ohwi) Yamazaki	+	+	Japan. Ryukyu Islands	*Yokota 3 Nov. 1997* (RYU)	AF509815	Albach et al. (in press a)
Veronicastrum stenostachyum (Helmsley) Yamazaki	+	+	China. Szechuan, cult. RBG Kew	*Lancaster 763* (K)	Albach & Chase (2001)	AF513354
Veronicastrum virginicum (L.) Farw.	+	+	U.S.A. Cult. RBG Kew	*Chase s.n.* (K)	Albach & Chase (2001)	Albach et al. (in press a)
Wulfenia carinthiaca Jacq.	+	+	Austria. Cult. BG Bonn	*Albach 74* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
Wulfeniopsis amherstiana (Benth.) D. Y. Hong	partial (450)	+	Pakistan	*Dickoree 13104* (GOET)	AF515216	Albach et al. (in press a)
			Veronica subg. *Veronica* (ca. 45 spp.)			
Veronica abyssinica Fresen.	+	−	Kenya. Cult. BG Bonn	*E. Fischer 728/98* (BONN)	Albach & Chase (2001)	—
Veronica abyssinica Fresen.	−	+	Rwanda	*E. Fischer 8060* (BONN)	—	AF513350
Veronica allionii Vill.	+	+	Italy. Cult. RBG Kew	Kew *1993–1463* (K)	AF509809	AF513348
Veronica alpina L.	+	partial (1259)	Sweden. Abisko NR	*Benson 1999.08* (UPS)	AF509810	AF511483/4
Veronica aphylla L.	partial (651)	+	Italy. Southern Tirol	*Zhang s.n.* (WU)	AF515211/2	AF513349

Table 1. Continued.

Species	ITS	*trn*L-F	Country. Locality	Voucher	ITS GENBANK	*trn*L-F GENBANK
Veronica bellidioides L.	+	+	Austria. Cult. RBG Kew	*Albach 118* (K)	Albach & Chase (2001)	AF513345
Veronica copelandii Eastw.	partial (332)	+	U.S.A. California	*Janeway 6557* (WU)	AF515213	AF513344
Veronica glandulosa Hochst. ex Benth.	+	+	Kenya. Cult. BG Bonn	*E. Fischer 713/98* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
Veronica japonensis Makino	+	+	Japan	*Stuessy et al. 17270* (WU)	AF509807	Albach et al. (in press a)
Veronica montana L.	+	+	Germany. Oberkassel	*Albach 151* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
Veronica morrisonicola Hayata	+	+	Taiwan. Cult. RBG Kew	*Kirkham & Flanagan 160* (K)	AF509808	AF513347
Veronica officinalis L.	+	+	England. Cult. RBG Kew	*Albach & Chase 114* (K)	Albach & Chase (2001)	Albach et al. (in press a)
Veronica scutellata L.	+	+	Austria. Waldviertel	*Dobes 7026* (WU)	AF509805	Albach et al. (in press a)
Veronica urticifolia Jacq.	+	+	cult. BG Bonn	*Albach 73* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
Veronica vandellioides Maxim.	+	+	China. Szechuan	*Dickoree 8417* (GOET)	AF509806	AF513346
Veronica wormskjoldii Roem. & Schult.	+	partial (1265)	U.S.A. Washington, Mt. Baker	*Olmstead 99–180* (WTU)	AF509811	AF511481/2
			Veronica subg. *Beccabunga* (ca. 40 spp.)			
Veronica acinifolia L.	+	+	Greece. Lefkas	*M. A. Fischer, Gutermann* (WU)	AF509798	Albach et al. (in press a)
Veronica beccabunga L.	+	+	England. Cult. RBG Kew	*Albach 122* (K)	Albach & Chase (2001)	Albach et al. (in press a)
Veronica gentianoides Vahl	+	+	cult. BG Bonn	*Albach 72* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
Veronica heureka (M. A. Fisch.) Tzvel.	+	+	Georgia. Greater Caucasus	*Albach 307* (WU)	AF509797	AF486404
Veronica peregrina L.	+	+	U.S.A. Montana	*Lesica 5668* (NY)	Albach & Chase (2001)	AF513352
Veronica serpyllifolia L.	+	+	Germany. Bonn	*Albach 64* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
			Veronica subg. *Pseudolysimachium* (ca. 35 spp.)			
Veronica longifolia L.	+	+	cult. BG Bonn	*Albach 66* (WU)	Albach & Chase (2001)	Albach et al. (in press a)

Table 1. Continued.

Species	ITS	*trn*L-F	Country. Locality	Voucher	ITS GENBANK	*trn*L-F GENBANK
Veronica dahurica Stev.	+	partial (830)	cult. BG Jena	*Albach s.n.* (WU)	Albach & Chase (2001)	AF511479/80
Veronica insularis Nakai	partial (441)	+	Korea. Ullung Islands	n.n. (WU)	AF515210	Albach et al. (in press a)
Veronica spicata L.	+	+	cult. BG Bonn	*Albach 65* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
			Veronica subg. *Synthyris* (18 spp.)			
Veronica missurica Raf. [= *Synthyris missurica* (Raf.) Pennell]	+	+	U.S.A. Oregon, cult. RBG Kew	*Albach 124* (K)	Albach & Chase (2001)	Albach et al. (in press a)
			Veronica subg. *Cochlidiosperma* (10 spp.)			
Veronica crista-galli Stev.	+	+	Georgia	*Dolmkanov 17.4.1983* (TBS)	AF509799	Albach et al. (in press a)
Veronica lycica E. Lehm.	+	+	Turkey. north of Kalkan	*Albach 269* (WU)	AF509802	AF513352
Veronica panormitana Tineo	+	+	Greece. Lefkas	*M. A. Fischer #9, 9 Apr. 1999* (WU)	AF509800	AF513330
Veronica sublobata M. A. Fisch.	+	+	U.K. Kew	*Albach 116* (K)	AF509803	Albach et al. (in press a)
Veronica trichadena Jord. & Fourr.	+	+	Greece. Lefkas	*M. A. Fischer #22, 9 Apr. 1999* (WU)	AF509801	AF513331
Veronica triloba (Opiz) Wiesbaur	+	+	Turkey. Aphrodisias	*Albach 242* (WU)	AF509804	AF513333
			Veronica subg. *Pellidosperma* (ca. 10 spp.)			
Veronica donii Römpp	+	+	Turkey. Between Cine and Yategan	*Albach 239* (WU)	AF509794	AF513351
Veronica glauca Sibth. & Sm.	+	−	cult. RBG Kew	*Kew 1973–14554* (K)	Albach & Chase (2001)	—
Veronica glauca Sibth. & Sm.	−	+	Greece. Lefkas	*M. A. Fischer #9, 7 Apr. 1999* (WU)	—	Albach et al. (in press a)
Veronica triphyllos L.	+	+	Turkey. Aphrodisias	*Albach 244* (WU)	AF509795	Albach et al. (in press a)
			Veronica subg. *Triangulicapsula* (2 spp.)			
Veronica chamaepithyoides Lam.	+	partial (891)	Spain	UA *174* (SALA)	AF509796	AF511477/8
			Veronica subg. *Stenocarpon* (ca. 30 spp.)			
Veronica ciliata Fisch.	partial (257)	+	China. Qinghai	*Miehe et al. 98-33313* (GOET)	AF515215	Albach et al. (in press a)

Table 1. Continued.

Species	ITS	*trn*L-F	Country. Locality	Voucher	ITS GENBANK	*trn*L-F GENBANK
Veronica fruticulosa L.	+	+	cult. BG Bonn	*Albach 71* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
Veronica lanuginosa Benth. ex Hook. f.	+	+	Nepal	*Dickoree 6482* (GOET)	AF509793	Albach et al. (in press a)
Veronica ruprechtii Lipsky	+	+	Georgia	*Sachokia 1 Sep. 1951* (TBS)	AF515214	Albach et al. (in press a)
Veronica thessalica Benth.	+	+	Greece. Thessalia	*Raus & Rogl 5072* (SALA)	AF509792	AF513343
			Veronica subg. *Chamaedrys* (ca. 10 spp.)			
Veronica arvensis L.	+	+	Germany. Bockenau	*Albach 147* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
Veronica chamaedrys L.	+	+	Norway. Cult. RBG Kew	*Albach 121* (K)	Albach & Chase (2001)	Albach et al. (in press a)
Veronica verna L.	+	+	Germany. Bad Kreuznach	*Albach 149* (WU)	AF509789	Albach et al. (in press a)
			Veronica subg. *Pocilla* (ca. 30 spp.)			
Veronica agrestis L.	+	+	Greece. Taygetos	*Albach 386* (WU)	AF509784	AF513335
Veronica amoena Bieb.	+	+	Georgia	*Schelkovnikov & Schmidt 5.4.1907* (TBS)	AF509786	AF513334
Veronica argute-serrata Regel & Schmalh.	+	+	Afghanistan	*Rechinger 35177* (WU)	AF509787	AF513337
Veronica campylopoda Boiss.	+	+	Jordan	*Schönswetter & Tribsch 4152* (WU)	Albach et al. (in press a)	Albach et al. (in press a)
Veronica filiformis Sm.	+	+	Georgia. Greater Caucasus	*Albach 298* (WU)	AF486363	Albach et al. (in press a)
Veronica persica Poir.	+	+	U.K. London	*Fay 175* (K)	AF509785	AF513336
Veronica polita L.	+	+	Germany. Martinstein	*Albach 146* (WU)	AF509818	Albach et al. (in press a)
Veronica rubrifolia Boiss.	+	+	Afghanistan	n.n. (WU)	AF509788	AF513338
			Veronica subg. *Pentasepalae* (ca. 75 spp.)			
Veronica bombycina Boiss. & Kotschy	+	+	cult. NYBG	*Struwe 1403* (WU)	Albach et al. (in press a)	Albach et al. (in press a)
Veronica bombycina subsp. *bolkar-daghensis* M. A. Fisch.	+	+	cult. NYBG	*Struwe 1406* (WU)	Albach et al. (in press a)	AF513342

Table 1. Continued.

Species	ITS	*trn*L-F	Country. Locality	Voucher	ITS GENBANK	*trn*L-F GENBANK
Veronica cuneifolia D. Don	+	+	cult. NYBG	*Struwe 1409* (WU)	Albach et al. (in press a)	Albach et al. (in press a)
Veronica czerniakowskiana Monjuschko	+	+	Iran	*Terme 39117E* (EVIN)	Albach et al. (in press a)	Albach et al. (in press a)
Veronica jacquinii Baumg.	+	+	cult. BG Bonn	*Albach 70* (WU)	Albach & Chase (2001)	AF513341
Veronica oltensis Woron.	+	+	cult. NYBG	*Struwe 1405* (WU)	Albach & Chase (2001)	AF513339
Veronica paederotae Boiss.	+	+	Iran. Prov. Mazandaran	*Klein 7901* (WU)	AF509783	AF513340
Veronica turrilliana Stoj. & Stefanov	+	+	Turkey. Istanbul	*Albach 278* (WU)	Albach et al. (in press a)	Albach et al. (in press a)
Outgroups (all Plantaginaceae, except *Oreosolen*—Scrophulariaceae)						
Digitalis obscura L.	partial (558)	+	Spain. Soria, cult. RBG Kew	*Chase 2469* (K)	AF515209	Albach et al. (in press a)
Erinus alpinus L.	+	+	Switzerland. near Evian	*Albach 158* (WU)	Albach & Chase (2001)	Albach et al. (in press a)
Globularia salicina Lam.	+	+	Canary Islands	*Chase 2547* (K)	Albach & Chase (2001)	AF513358
Lafuentea rotundifolia Lag.	+	+	Spain	*Martínez-Ortega 889* (SALA)	AF509816	AF513356
Oreosolen wattii Hook. f.	+	+	China. Xizang	*Dickoree 5182* (GOET)	AF509817	AF513357
Plantago coronopus L.	partial (432)	+	U.K. Cheshire	*Chase 2763* (K)	AF515217	Albach et al. (in press a)
Plantago cretica L.	+	+	Cyprus. Protaras	*Albach 126* (WU)	Rønsted et al. (2002)	AY101955
Plantago lanceolata L.	+	−	cult. RBG Kew	*Chase 2765* (K)	Albach & Chase (2001)	—
Plantago lanceolata L.	−	+	cult. BG Copenhagen	*Rønsted 33* (C)	—	Rønsted et al. (2002)
Plantago major L.	+	+	cult. BG Halle	*Rønsted 41* (C)	Rønsted et al. (2002)	Rønsted et al. (2002)
Plantago uniflora L.	partial (617)	+	U.K. Cumberland, cult. RBG Kew	*Chase 2798* (K)	AF515218	Rønsted et al. (2002)
Sibthorpia europaea L.	+	+	cult. RBG Kew	*Albach 125* (K)	Albach & Chase (2001)	AF513355

dition with tree bisection reconnection were conducted multiple times (usually 3 times) with MulTrees (keeping multiple shortest trees) in effect with no tree limit. Bootstrap percentages were estimated using 500 replicates and SPR-branch swapping with a maximum of 20 trees per replicate to assess support for relationships. Branch support was also estimated with a decay (Bremer support) analysis using AutoDecay vers. 4.0 (Eriksson, 1998) with simple taxon addition and TBR branch swapping, saving all most parsimonious trees. A third method to estimate confidence in the tree is based on Bayesian statistics as implemented in the computer program MrBayes 2.01 (Huelsenbeck & Ronquist, 2001). We used default settings with a GTR+Γ likelihood model and started the analysis from a random tree. Four Markov chains, three heated and one cold chain, were run simultaneously for 200,000 generations each and the current tree saved every 10 generations. To check that stationarity had been reached we plotted the likelihood values per generation and repeated the simulation twice. The first 3000 generations were discarded (burn-in). A majority-rule consensus showing all compatible groupings of the resulting 19,700 trees was then used to show approximate posterior probabilities that the clade exists. For character analysis, we have used MacClade 3.06 (Maddison & Maddison, 1992).

Incongruence between nuclear and plastid DNA sequences is a widespread phenomenon and may have various causes (Wendel & Doyle, 1998), for example, hybridization and introgression (Soltis et al., 1996). The data sets were therefore analyzed both separately and in combination to test for congruence. Bootstrap support was estimated for separate and combined data sets. We here do not discuss results of soft incongruence (sensu Seelanan et al., 1997) in which the two data sets show different relationships but only one gives more than 50 BP (bootstrap percentage) for this relationship. Those cases herein in which the individual analyses support different results, however, indicate sources of true incongruence and will be discussed in more detail.

One reason for incongruence may be homoplasy in at least one data set. CT transitions are the most common nucleotide change in ribosomal DNA due to the spontaneous deamination of C to U occurring in nature, a mutation that in contrast to other mutations maintains RNA base pairing (Vawter & Brown, 1993; Hershkovitz et al., 1999) and is, therefore, more likely to be retained. Soltis and Soltis (1998) investigated the effect of down-weighting transversions in the analysis of 18S rDNA. They found, however, only a decrease in the resolution of the strict consensus trees and concluded that a down-weighting of transversions is probably not worth the effort of extra computer time required to conduct some of the analyses (Soltis & Soltis, 1998: 205). We have analyzed our ITS data set separately and combined with the *trn*L-F data set parallel to the unweighted analysis with CT transitions removed from the data set using a step matrix to test the effect of CT transitions in ITS on the results.

Results

The analysis of the nrITS-region included 915 characters, 335 of them potentially parsimony informative, and resulted in 864 most parsimonious trees of 2199 steps with a consistency index (CI) of 0.37 and a retention index (RI) of 0.66 (Fig. 1). The results of the analysis of ITS are very similar to those by Albach and Chase (2001). However, resolution of the major subclades of *Veronica* is lower. *Paederota*, *Synthyris*, and the Hebe complex are nested within *Veronica*. *Veronica* subg. *Beccabunga* is the first branching subclade in *Veronica*. The position of subgenus *Cochlidiosperma* differs between the analyses of the two DNA regions. It is sister to subgenera *Pentasepalae*, *Pocilla*, and *Chamaedrys* in Albach and Chase (2001), whereas it is sister to the subgenus *Pseudolysimachium* here (Fig. 1).

The analysis of the *trn*L-F including 1336 characters, 333 of them potentially parsimony informative, was run several times with a tree limit of 1000 trees. Trees from one replicate were saved. They included 1183 steps with CI = 0.66 and RI = 0.81 (Fig. 2). The results of the analysis of the *trn*L-F region are very similar to those of Albach et al. (in press a). Resolution of the major subclades in *Veronica* increased, in contrast to results from ITS. *Paederota* and *Picrorhiza* are sister to *Veronica* in both analyses, whereas *Synthyris* and the Hebe complex are again nested within *Veronica*. Subgenus *Veronica* is the first branching subclade in *Veronica* (Fig. 2), whereas it was in a basal polytomy in Albach et al. (in press a). The Hebe complex is again sister to subgenera *Pentasepalae* and *Pocilla*.

The favored method of examining incongruence among two or more data sets is comparison of separate and combined results on a node-by-node basis, specifically bootstrap support and resolution. Taxa of *Veronica* that appear in different positions in the two separate analyses are not well supported in both analyses and are therefore not considered true incongruences but most likely due to sampling error (Reeves et al., 2001). This was also confirmed by incongruence tests performed by Albach and

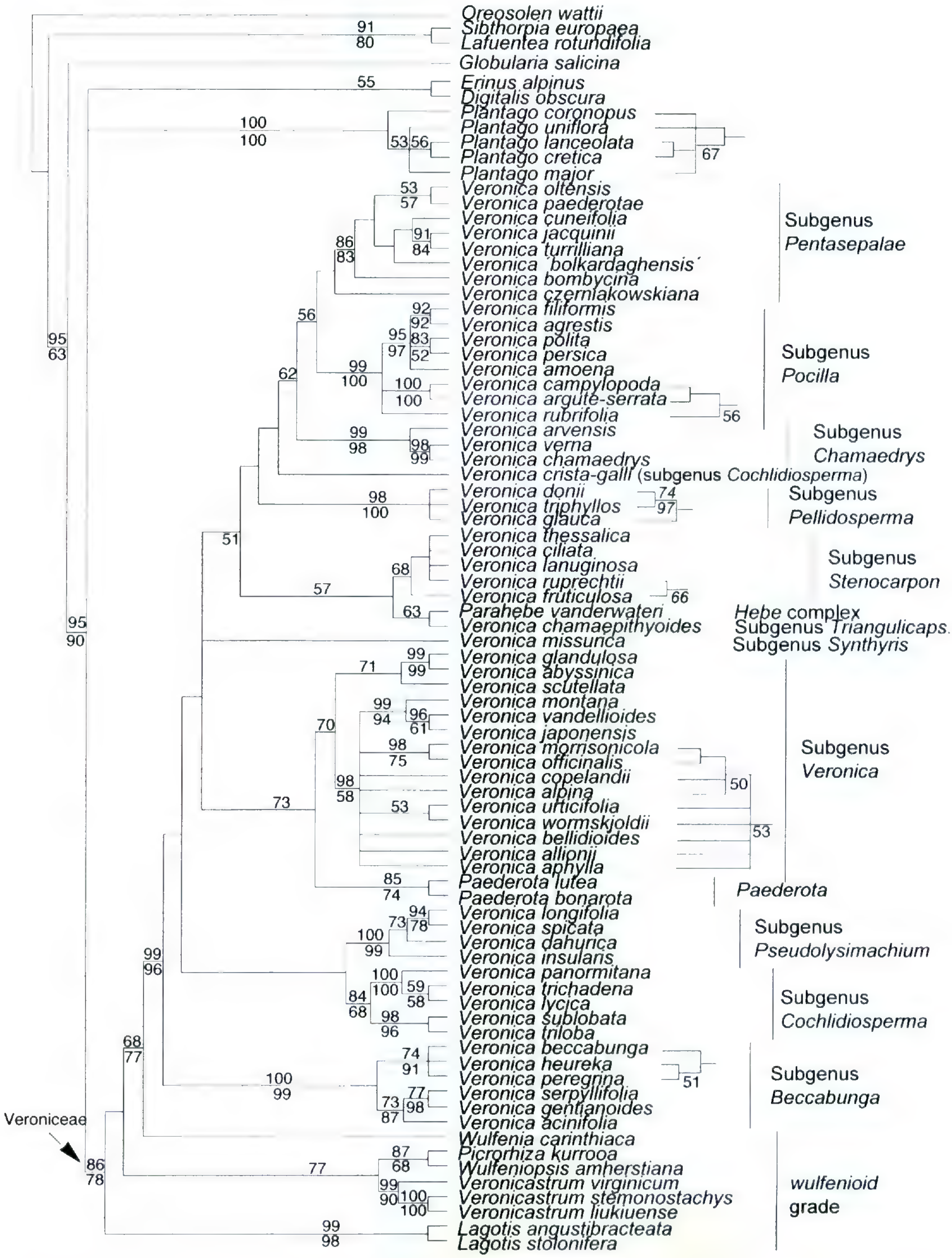

Figure 1. Strict consensus tree of 864 most parsimonious trees of the analysis of the ITS data set. Numbers above the branches indicate bootstrap percentages for the analysis of equally weighted characters. Numbers below the branches indicate bootstrap percentages for the analysis of characters excluding CT transitions. Relationships to the right of the species names show relationships found in the bootstrap analyses but not found in any most parsimonious tree. CI = 0.37; RI = 0.66. *Veronica* "*bolkardaghensis*" is an abbreviation for *Veronica bombycina* subsp. *bolkardaghensis*.

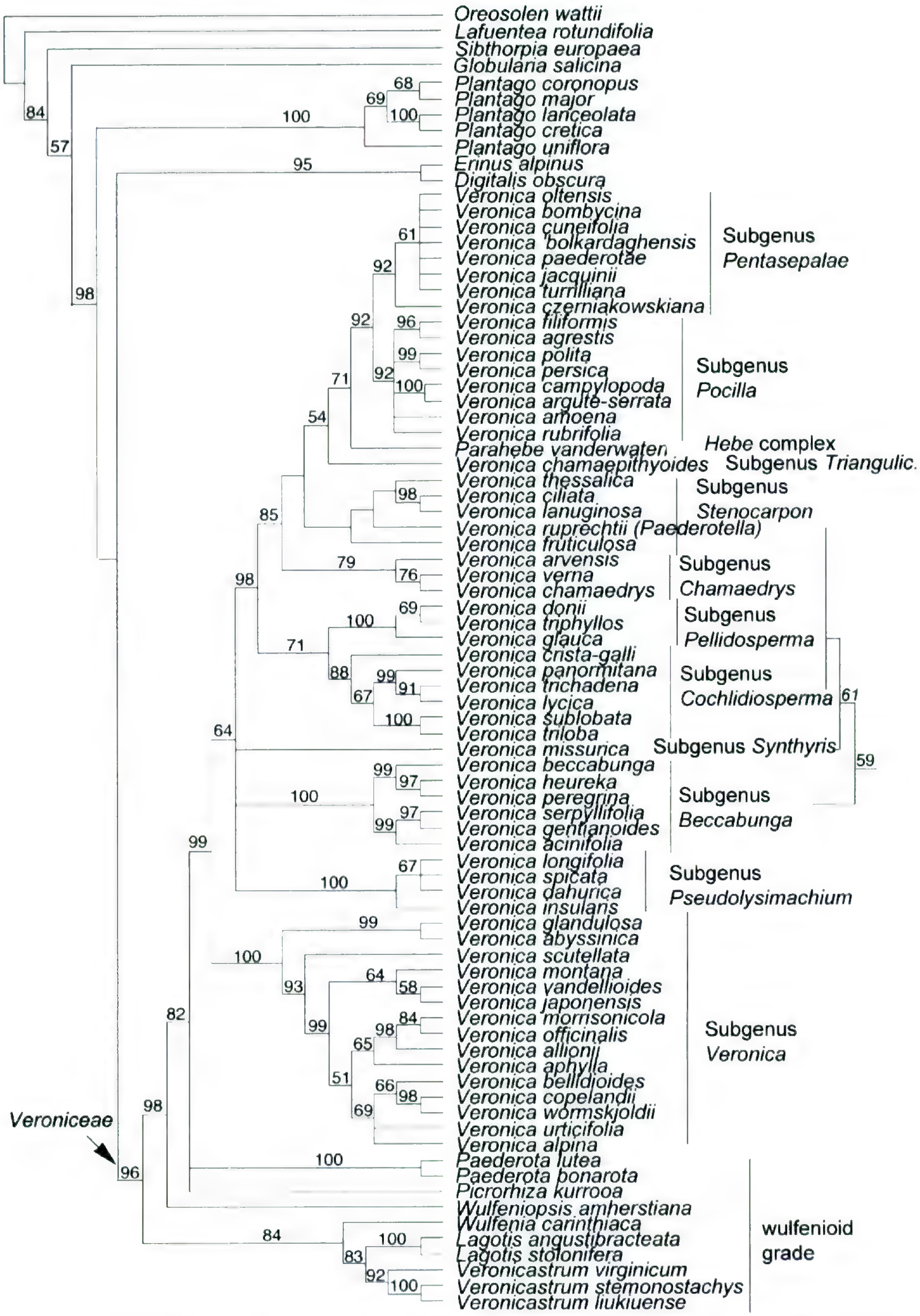

Figure 2. Strict consensus tree of 1000 most parsimonious trees of the analysis of the *trn*L-F data set. Numbers above the branches indicate bootstrap percentages for the analysis of equally weighted characters. Relationships to the right of the species names show relationships found in the bootstrap analyses but not found in any most parsimonious tree. CI = 0.66; RI = 0.81. *Veronica* "*bolkardaghensis*" is an abbreviation for *Veronica bombycina* subsp. *bolkardaghensis*.

Chase (in press). However, the relationships among the members of the wulfenioid grade appear to be cases of true incongruence, with results from ITS and *trn*L-F differing strongly due to hybridization (Albach & Chase, in press). Based on the lack of true incongruence among members of *Veronica*, we decided to combine the matrices and to discuss differing inferences based on the two different hypotheses, if appropriate.

The combined data matrix included 2251 characters, 668 of them potentially parsimony informative. The analysis resulted in 112 most parsimonious trees of 3431 steps (CI = 0.47; RI = 0.70; Fig. 3). Tree scores estimated separately for the two individual partitions differ considerably. ITS accounts for 2219 to 2222 steps, whereas *trn*L-F accounts for 1210 to 1213 steps of the total 3431 steps. The CI of the ITS partition was 0.37 and the RI = 0.65, whereas for the *trn*L-F partition CI = 0.64 and RI = 0.80. These values are similar to those from separate analyses previously published (Albach & Chase, 2001; Albach et al., in press a). The combined analysis shows better resolution and higher bootstrap support than the analysis of the two partitions alone. In some patterns it resembles the results from the ITS analysis (e.g., Hebe complex sister to subg. *Stenocarpon*), whereas in others it resembles the *trn*L-F analysis (e.g., *Paederota* sister to *Veronica* s.l.). The sister-group relationship of subgenus *Synthyris* and subgenus *Beccabunga* is not found in either strict consensus tree of the individual regions (Figs. 1, 2). Support for the monophyly of subgenera *Stenocarpon* and *Cochlidiosperma* is increased compared with analyses of separate data sets. Generally, we can state that all strongly supported clades of the combined analysis represent relationships supported consistently in all individual analyses.

CT transitions are by far the most common character change in the data set (815 steps compared with 427 steps for AG transitions and 348 steps for AC transversions) as reported for rDNA generally (Vawter & Brown, 1993; Hershkovitz et al., 1999), although they are not the most frequent nucleotides (21.4% A, 28.6% C, 29.0% G, 21.1% T). However, CT transitions are not only the most common character change, but also have the lowest consistency index, although the effect is not large. The exclusion of CT transitions from the data leads to a slight increase of the CI and RI (0.37 to 0.41 and 0.66 to 0.68, respectively). The exclusion of AG transitions (CI = 0.33; RI = 0.63) and AC transversions (CI = 0.33; RI = 0.64) leads to a decrease in the tree scores. Our investigation of the effects of removing CT transitions corroborated the results of Soltis and Soltis (1998) in 18S rDNA of mainly decreased resolution. The analysis with this pruned ITS data set had to be run with a tree limit of 5000 trees, which had 1267 steps with CI = 0.42 and RI = 0.69 (Fig. 4). Branch support similarly decreases after removal of CT transitions, although a few relationships find increased support (e.g., sister-group relationship of *V. donii* and *V. triphyllos*, from 74 BP to 97 BP). These relationships concern especially species groups in which taxon sampling is poor, such as *Veronica* subg. *Beccabunga*, thus preventing the detection of homoplasy in the phylogenetic analysis. All supported clades of the ITS analysis with a conflicting supported relationship in the *trn*L-F analysis are not supported in the analysis of ITS with removed CT transitions, with the exception of the *Veronica* + *Paederota* + *Wulfenia* clade.

Consequently, support for clades in the combined analysis with CT transitions removed from the ITS partition is higher for many clades than in the equally weighted combined analysis because of the greater weight of *trn*L-F characters. Those clades with lower support represent mainly cases in which ITS with removed CT transitions and *trn*L-F are not variable enough. An especially noteworthy relationship in this combined analysis with CT transitions removed from the ITS partition is the sister-group relationship of subgenus *Veronica* to the rest of *Veronica* (no support in the combined analysis, 64 BP in *trn*L-F, 87 BP in the combined analysis with CT transitions removed from the ITS partition).

Bootstrap analysis (Fig. 3) and Bayesian statistics support mostly the same relationships (Fig. 5) with posterior probabilities being higher than bootstrap percentages in all cases in which bootstrap percentages are below 95, as noted by Buckley et al. (2002). However, there are some notable differences. Bayesian maximum likelihood does not support the monophyly of the combined clade of subgenera *Cochlidiosperma* and *Pellidosperma* and supports positions of subgenus *Synthyris* and *Veronica scutellata* as shown in the analysis with CT transitions removed from the ITS partition (Fig. 4), albeit with probabilities below 90%. Most interesting are the inferred relationships in the wulfenioid grade. Here (Fig. 5), Bayesian maximum likelihood supports the position shown in the analysis of ITS (Fig. 1) rather than the *trn*L-F (Fig. 2) and combined analysis (Fig. 3). The analysis with CT transitions removed from the ITS partition (Fig. 4) was largely unresolved in the wulfenioid grade. Nevertheless, we base our following discussion on the simple combined analysis (Fig. 3) but discuss in-

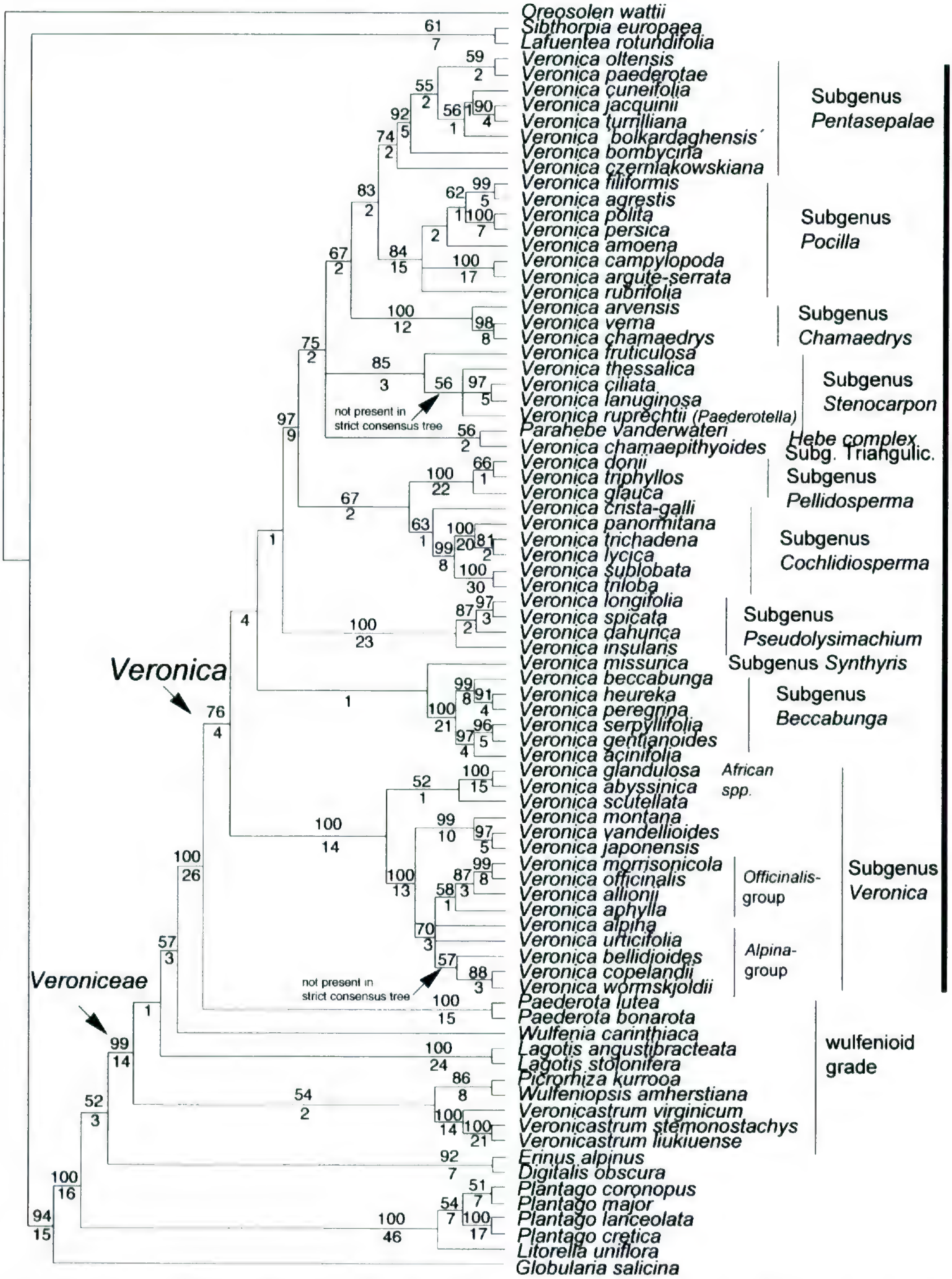

Figure 3. Strict consensus tree of 112 most parsimonious trees of the analysis of the combined data set of the nrITS and *trn*L-F regions. Numbers above the branches indicate bootstrap percentages for the analysis of equally weighted characters. Numbers below branches indicate decay value (Bremer support). CI = 0.47; RI = 0.70. *Veronica* "*bolkardaghensis*" is an abbreviation for *Veronica bombycina* subsp. *bolkardaghensis*.

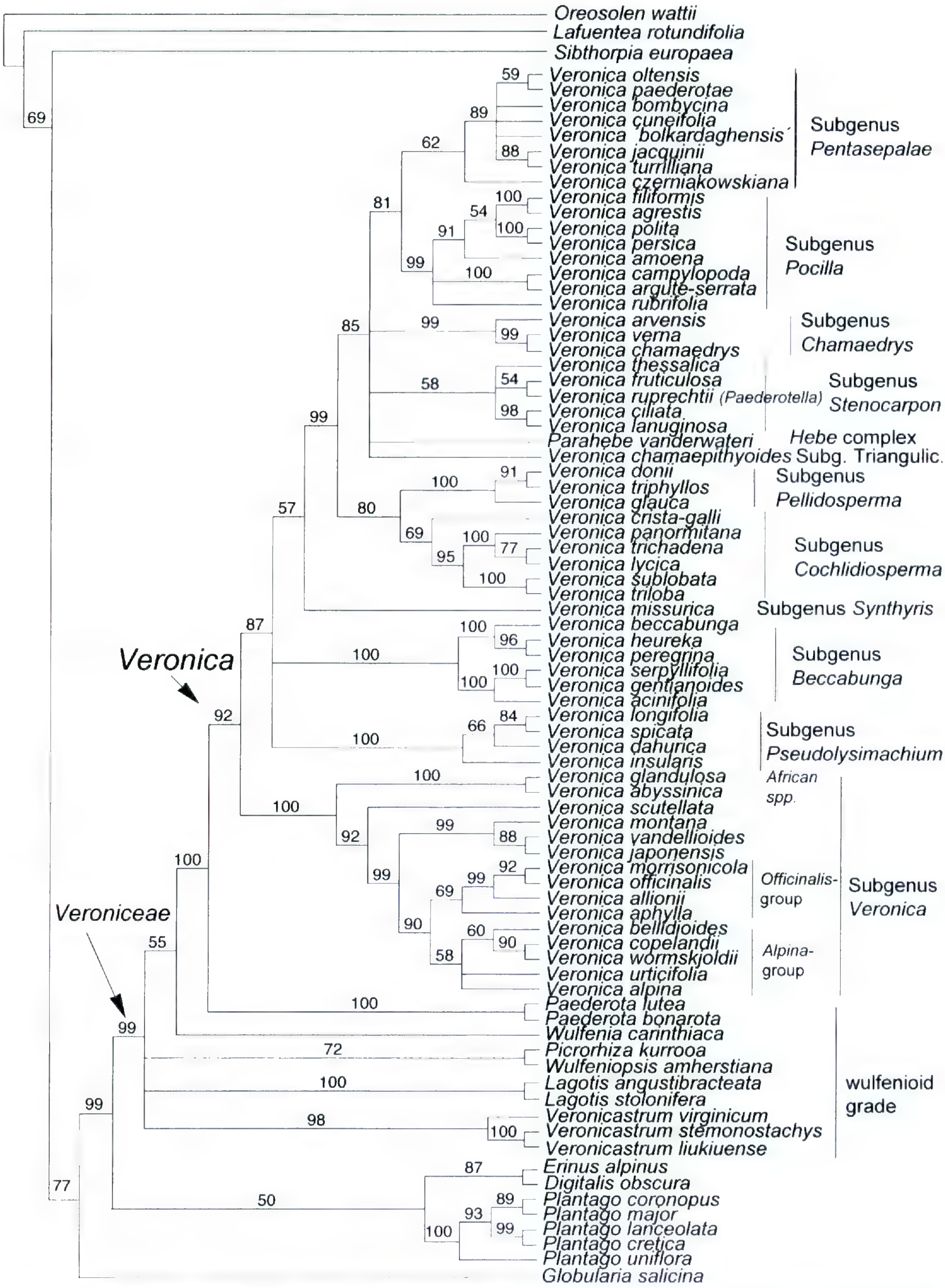

Figure 4. Strict consensus tree of 5000 most parsimonious trees of the analysis of the combined data set excluding CT transitions in the ITS partition. Numbers above the branches indicate bootstrap percentages for the analysis of equally weighted characters. CI = 0.42; RI = 0.69. *Veronica* "*bolkardaghensis*" is an abbreviation for *Veronica bombycina* subsp. *bolkardaghensis*.

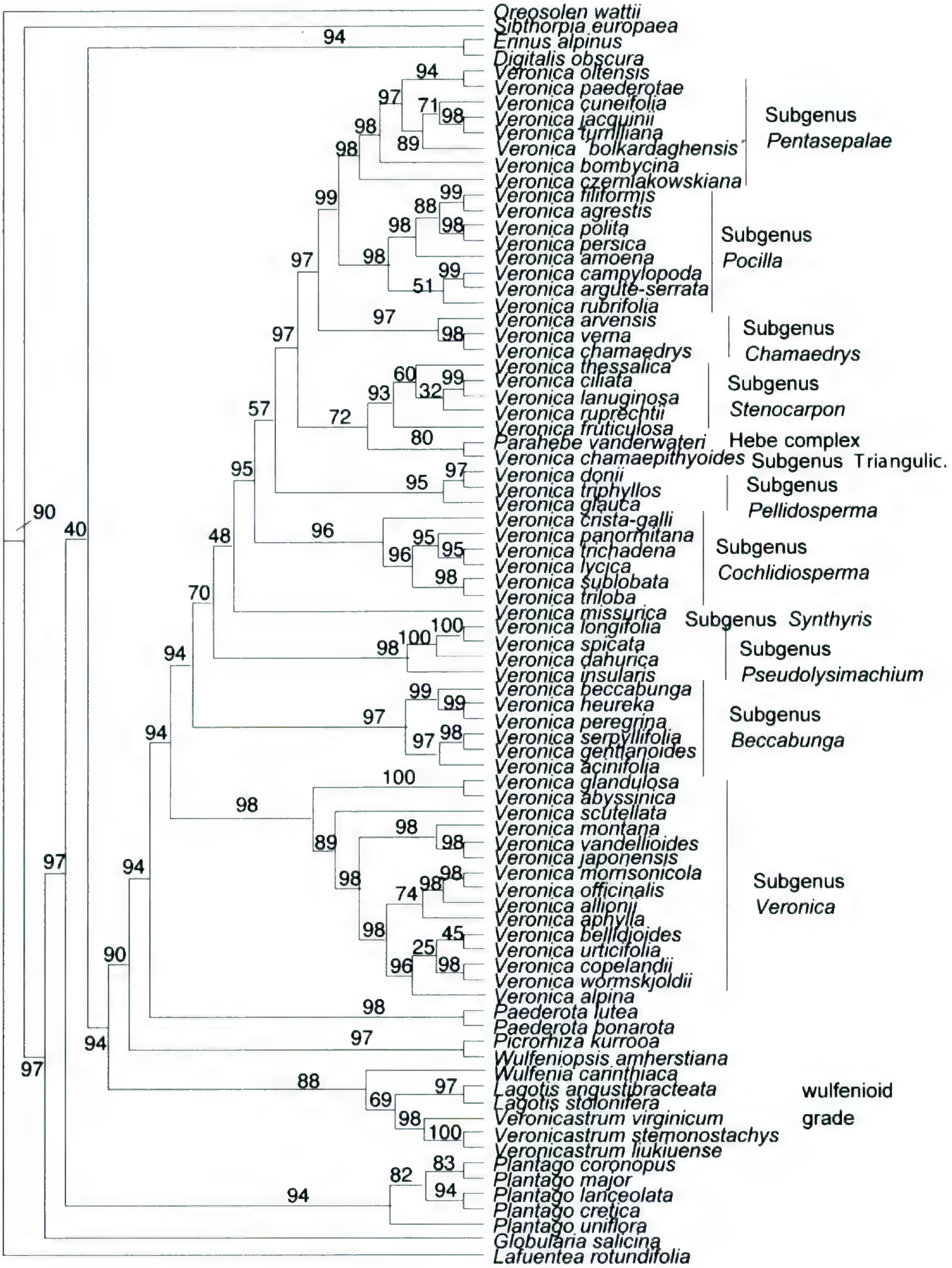

Figure 5. Majority-rule consensus including all compatible groupings from 19,700 trees of the Bayesian maximum likelihood analysis. Numbers above the branches represent percent recoveries and can be translated as posterior probabilities. *Veronica* "*bolkardaghensis*" is an abbreviation for *Veronica bombycina* subsp. *bolkardaghensis*.

ferences from other relationships suggested by the analysis with CT transitions removed from the ITS partition or supported by Bayesian maximum likelihood if necessary.

Discussion

The combined analysis of ITS and *trn*L-F gives us the most robust phylogeny of Veroniceae to date. In the following, we will compare this phylogeny with information about structural data, mainly from the literature. This analysis is restricted to the most important characters, due to space limitations. For a more comprehensive discussion, the reader is referred to Albach (2002). Furthermore, the evolution of the seeds will be discussed in a separate paper (Martínez-Ortega & Albach, in prep.). While discussing these characters, we should be aware that this phylogeny does not include all species and therefore may be misleading. Our taxon sampling was designed to minimize this effect but could not exclude it completely. Additionally, the results of the combined analysis are based on conflicting data in the wulfenioid grade (see above), which may lead to different inferences. We have discussed these problems where necessary.

Vegetative Morphology

One of the main differences recognized in plant morphology is whether the main shoot continues growth (monopodium) or is substituted by a lateral off-shoot in the next season (sympodium). Veroniceae are variable in this character, and some species do both. Mapping this character on one of our most parsimonious trees (result not shown) shows that strict monopodial growth is most likely plesiomorphic for Veroniceae and was subsequently lost twice, once in *Veronicastrum* and once in the clade formed by *Paederota* and *Veronica*. In *Veronicastrum*, *Paederota*, and most species of *Veronica*, the shoot apex dies back after the flowering season and new shoots arise from lateral buds in the lower, vegetative region (Hamann, 1958). Within *Veronica*, some species have been found (*V. officinalis*, *V. beccabunga*, *V. aphylla*, *V. montana*, *V. cuneifolia*, *V. filiformis*, Hamann, 1958; *V. caespitosa*, *V. bombycina*, *V. thessalica*, Fischer, 1969) that either reverted to monopodial growth, or kept it and the terminal shoot continues to grow in the next season. Possibly, even more are able to grow monopodially but have not yet been investigated, e.g., East Asian species of subgenus *Veronica*, such as *V. piroliformis*. Fischer (1969) hypothesized a phylogenetic importance of prolification (innovation of a terminal shoot normally discontinued). A comparison with our phylogenetic hypothesis, however, does not show prolificating species to be closely related. Prolification is associated in *Veronica* with a plagiotropous stature and the lack of a terminal inflorescence. The only exception is *V. filiformis*, which is the only perennial member of the otherwise nonprolificating annual subgenus *Pocilla*. All species of this subgenus have a terminal inflorescence (see discussion under inflorescence morphology). The development of a shoot from the terminal inflorescence in *V. filiformis* is, therefore, one possibility to continue growth otherwise limited by a terminal inflorescence (Lehmann, 1942; Thaler, 1951; Hamann, 1958). In *V. filiformis* prolification may have been the only possibility to continue growth, because the vegetative part had been reduced in its annual ancestor and lateral buds were few or lacking.

Pennell (1935) and Thieret (1955) arranged Veroniceae in two series, one with cauline leaves and the other with a basal rosette. Hong (1984) rejected this arrangement, citing a correlation of alpine and subalpine habitats with a basal rosette (see also Körner, 1999). Species of *Veronica* subg. *Synthyris* outside alpine regions may, therefore, have evolved from more alpine ancestors from which they inherited their rosette form. However, species of *Veronica* subg. *Synthyris* and other species of *Veronica* differ from other Veroniceae with basal rosettes, such as *Wulfenia*, in having the rosette on the flowering stem and growing sympodially, whereas some species of *Veronica*, *Wulfenia*, and also *Plantago* have a terminal rosette with axillary inflorescences (monopodium). It is noteworthy that *Plantago*, the inferred sister to Veroniceae in several broad-scale phylogenetic analyses of DNA sequence data (Olmstead & Reeves, 1995; Oxelman et al., 1999; Olmstead et al., 2000, 2001; Albach et al., 2001), also seems to have evolved from an ancestor growing monopodially with a basal rosette (Rahn, 1996). A common origin of these basal rosettes, however, implies that *Aragoa*, observed as sister to *Plantago* (Bello et al., 2002), has lost its basal rosette. Within the Officinalis group of subgenus *Veronica*, we have a morphological transition series from a prolificating species (*Veronica officinalis*) via an intermediate with a large shoot apex (*V. grandiflora*) to a rosette species with a stunted shoot apex and pseudoterminal inflorescence (*V. aphylla*).

Inflorescence Morphology

The inflorescence morphology, especially the presence or absence of a terminal inflorescence, has been one of the main characters to divide *Ve-*

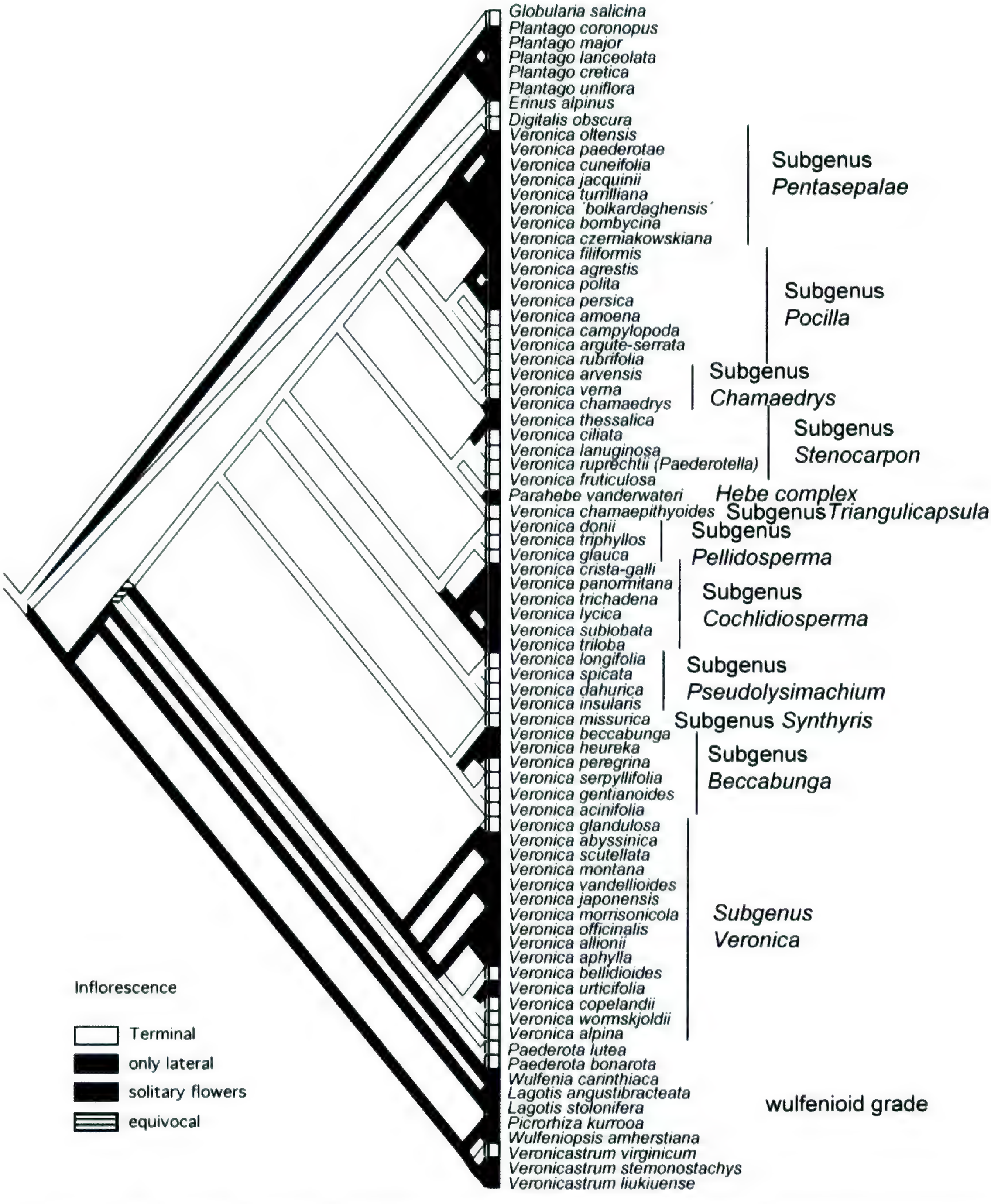

Figure 6. Occurrence of a terminal inflorescence mapped on one most parsimonious tree from the combined analysis (ACCTRAN optimization). *Veronica* "*bolkardaghensis*" is an abbreviation for *Veronica bombycina* subsp. *bolkardaghensis*.

ronica infragenerically in previous classifications (Römpp, 1928; Elenevskij, 1977). We have discussed earlier (Albach & Chase, 2001; Martínez-Ortega & Rico, 2001) that this character is more plastic than previously assumed. Mapping the presence of a terminal inflorescence on one of our most parsimonious trees (Fig. 6) indicates that the ancestral condition is the absence of a terminal inflorescence and that the presence of a terminal inflorescence has evolved at least five times, in *Veronicastrum virginicum* and relatives, in *Paederota*, in the Alpina group and in *Veronica glandulosa* of subgenus *Veronica*, and in the remainder of *Veronica*. In subgenus *Veronica* the character has been apparently labile (Fig. 6), whereas it became apparently more canalized in the rest of *Veronica*

s.l. A different interpretation is possible considering that a terminal inflorescence is correlated with an annual life history (Hamann, 1958; Albach et al., in press a) and also often with alpine habitats. Most of the alpine species with only lateral inflorescences evolve a pseudoterminal condition (Fischer, 1969; also in the montane *V. urticifolia*, Hamann, 1958). *Veronica aragonensis* is a good example, because these alpine dwarf plants have typically pseudoterminal inflorescences, but plants from lower altitudes have clearly axillary racemes (Montserrat, 1968). In alpine species a seemingly terminal inflorescence, which is derived either by a truly terminal inflorescence or a pseudoterminal inflorescence with a degenerated shoot apex, seems to be favored by selection. A truly terminal inflorescence may have evolved multiple times due to selection pressure in these habitats from a proto-*Veronica* and -*Paederota* with only lateral inflorescences. Following this argument, the transition from the lack of a terminal inflorescence to its presence is more likely than vice versa in the phylogenetic history of *Veronica*, due to the repeated invasion of alpine habitats and shifts to an annual life history.

Solitary flowers in the Agrestis group and subgenus *Cochlidiosperma* evolved in parallel. These "solitary" flowers are subtended by leaf-like bracts in contrast to a gradual change of leaf shape within the inflorescence (e.g., *V. tenuifolia* Asso, *V. ponae* Gouan) or scale-like bracts (e.g., *V. glauca*, *V. spicata*) in other species. Hamann (1958), however, concluded that the flower subtending leaves in the Agrestis group and subgenus *Cochlidiosperma* are foliaceous bracts, and these species do not have solitary flowers but terminal inflorescences. This was based on the observation that phyllotaxy in the inflorescence and the vegetative part of the plant differ—opposite in the vegetative parts and alternate in the inflorescence. Indeed, an ancestor with a terminal inflorescence is inferred for both clades with solitary flowers (Fig. 6), suggesting that in both cases evolution proceeded toward enlarged bracts compensating for reduced vegetative parts and elongation of internodes in terminal inflorescences.

FLOWER DEVELOPMENT

The most obvious character of *Veronica* is its tetramerous short-tubed flower. However, despite several descriptions of flower development in single species (e.g., Noll, 1883, for *V. longifolia*), comparative studies of flower development have been lacking. Only the study by Kampny and Dengler (1997) provided comparable data for several species (*Veronica chamaedrys*, *V. serpyllifolia*, *V. longifolia* [= *Pseudolysimachion longifolium*], *V. regina-nivalis* [= *Synthyris reniformis*], *V. besseya* [= *Besseya alpina*], the latter two from subgenus *Synthyris*, *Hebe parviflora* (subg. *Hebe*), *Derwentia perfoliata* (subg. *Derwentia*), *Wulfenia carinthiaca*, *Veronicastrum virginicum*, *Digitalis grandiflora*, and *Verbascum blattaria*).

Stamens are initiated simultaneously with or before corolla initiation in all Veroniceae (Kampny & Dengler, 1997). Development of the stamens is initiated before the corolla in the short-tubed flowers of the Veroniceae (Fischer, 1920). The gynoecium is initiated at the same time as the corolla. This is consistent with a delayed onset of corolla tube development leading to its reduced size. Kampny and Dengler (1997) found similarity in the speed of flower part development of *Veronica serpyllifolia* and subgenus *Synthyris*. For example, calyx lobe growth is slowed just before anthesis, whereas its growth is slowed at an earlier stage in the Hebe complex. Calyx lobe growth is continuous in subgenus *Pseudolysimachium* and *Veronica chamaedrys*, and decreases gradually in *Veronicastrum*. A comparison of developmental timing also shows that the tubular flower of *Veronicastrum*, *V. longifolia*, and the Hebe complex developed differently, and they are thus not homologous (Kampny et al., 1994; Kampny & Dengler, 1997). Corolla tube growth terminates just before anthesis in *Veronicastrum*, whereas growth slows at an earlier stage in the Hebe complex, probably because the mechanism allowing corolla tube growth at a later stage was lost in the short-tubed ancestors of the Hebe complex. Flower development in Veroniceae is, as can be seen from these examples, a mixture of heterochronic events of increasing and decreasing speeds, earlier and delayed onsets, and terminations of development (Kampny et al., 1993). This mixture of heterochronic events is not restricted to a few long-tubed species but is also apparent in other species of *Veronica*, in which relation of corolla tube to corolla lobes is not identical but can vary from 2:5 to 1:8 (Aseyeva, 2002).

CALYX

In the calyx and corolla, reductions in the number of lobes from five to four have occurred. Reductions in the two kinds of whorls are not correlated and therefore necessitate separate discussions. Reduction in calyx lobe number is due to loss of the posterior lobe, whereas that in corolla lobes is due to congenital fusion. Reduction in calyx lobe number characterizes *Veronica* s.l. Reversals to five calyx lobes, on the other hand, need to be hypothe-

sized for *Veronica* subsect. *Austriacae* (Wulff) Riek (i.e., *V. jacquinii, V. turrilliana*), *V. ruprechtii* (*Paederotella*), "Chionohebe" and some other isolated species in subgenera *Veronica, Pentasepalae, Stenocarpon,* and the Hebe complex. However, the pentasepalous flower is not constant within species (even within individuals!) of *Veronica* subsect. *Austriacae,* nor is the tetrasepalous flower constant in the remaining species (Lehmann, 1918). Furthermore, there is a distinction in the pentasepalous state of *Veronicastrum* and *Veronica* subsect. *Austriacae,* because in the former the posterior sepal is formed as the third sepal and well before the corolla, whereas in the latter it is formed after the corolla (Fischer, 1920). There is some variation in the formation of front and back sepals (Fischer, 1920), but sufficient data to allow any inference are lacking. Further investigation into the development of the calyx in Veroniceae and *Plantago* seems necessary to test the homology of tetramerous calyces in the two groups. Investigations up to now indicate non-homology due to the loss of the fifth sepal in Veroniceae and, in contrast, fusion of two lobes into the ventral lobe in *Plantago lanceolata* (Henderson, 1926).

COROLLA

Apart from the reduction in calyx lobe number, we also find a reduction in number of corolla lobes from five to four. Whereas the reduction in calyx lobe number is not stable, the tetrapetalous flower in *Veronica* is rather stable (Lehmann, 1918). Exceptions occur in "Besseya" (subg. *Synthyris*), where the corolla is lost, and *V. ruprechtii* (= *Paederotella pontica*; probably subg. *Stenocarpon*), "Detzneria," and "Chionohebe" (subg. *Hebe*) with pentapetalous corollas. However, corolla lobe number can vary between two and eight within individuals and populations in a few species (like *V. fruticans*), sometimes remarkably frequently (pers. obs.). A pentamerous (and tetraploid) form of *V. erinoides* has been the basis of a new species (Contandriopoulos & Quézel, 1964), though it is probably nothing more than an aberrant, teratological small population (according to Fischer, 1991). Traditionally, a pentamerous corolla has been overrated as a diagnostic character in *Veronica.* Outside *Veronica,* the tetrapetalous corolla occurs in *Picrorhiza scrophulariiflora, Veronicastrum, Scrofella, Wulfeniopsis,* and *Paederota. Lagotis* is extremely variable in this respect, having most commonly three corolla lobes. Mapping this character on the molecular tree (result not shown) implies a tetramerous corolla in the ancestor of Veroniceae and reversals in *Picrorhiza kurrooa, Wulfenia* (and *Kashmiria*), some African species of *Veronica, V. ruprechtii,* "Detzneria," and "Chionohebe." The sister-group relationship of Veroniceae and the tetramerous *Plantago* hypothesized in most analyses of molecular data sets (Olmstead & Reeves, 1995; Oxelman et al., 1999; Olmstead et al., 2000, 2001; Albach et al., 2001) and the sister-group relationship of *Aragoa* and *Plantago* (Bello et al., 2002) indicated that tetramery may be plesiomorphic in the clade of *Plantago* and *Veronica.* Reeves and Olmstead (1998) first speculated about a common origin but emphasized the need for increased taxon sampling. With the increased taxon sampling here, we still infer the common origin of a tetramerous corolla in the clade of *Plantago, Aragoa,* and Veroniceae if *Digitalis* and *Erinus* are sister to this clade. However, there might also have been just a tendency for corolla lobes to fuse in the earliest species of *Plantago* and Veroniceae; these species could then have been the ancestors of multiple species with tetramerous corollas. Thus, a predisposition to form tetramerous flowers would be a synapomorphy for the clade containing *Plantago* and Veroniceae.

The fusion of corolla lobes in *Veronica* involved the two adaxial corolla lobes. This fusion is more or less complete, with some corollas still showing a notch in the adaxial corolla lobe. In those flowers without a notch we may still find two nerves in the one adaxial corolla lobe as a relic of the two separate lobes, whereas in others fusion is more complete and only one nerve is present (Lehmann, 1918). Vascular patterns were studied in detail by Saunders (1934), who showed that the reduction from five corolla lobes to four preceded the reduction from two to one midrib in the adaxial lobe derived from the fusion, and that the reduction to one midrib was incompatible with the occurrence of a fifth sepal. A comparison with the classification of that time gave a confusing picture of multiple parallel evolutionary trends (Saunders, 1934). A comparison of the data from Saunders (1934), together with additional information by Aseyeva (2002) and our molecular hypothesis, however, gives a much clearer picture (Fig. 7). The reduction to a single midrib is strictly confined to three clades—subgenus *Pseudolysimachium,* subgenus *Beccabunga,* and subgenera *Cochlidiosperma* plus *Pellidosperma* (but not in *V. crista-galli*), although Aseyeva (2002) reported a single midrib also from *V. biloba* (subg. *Pocilla,* not sampled in our analysis). The most parsimonious interpretation is then a reversal in the clade of subgenera *Pentasepalae, Pocilla, Chamaedrys, Stenocarpon, Derwentia,* and

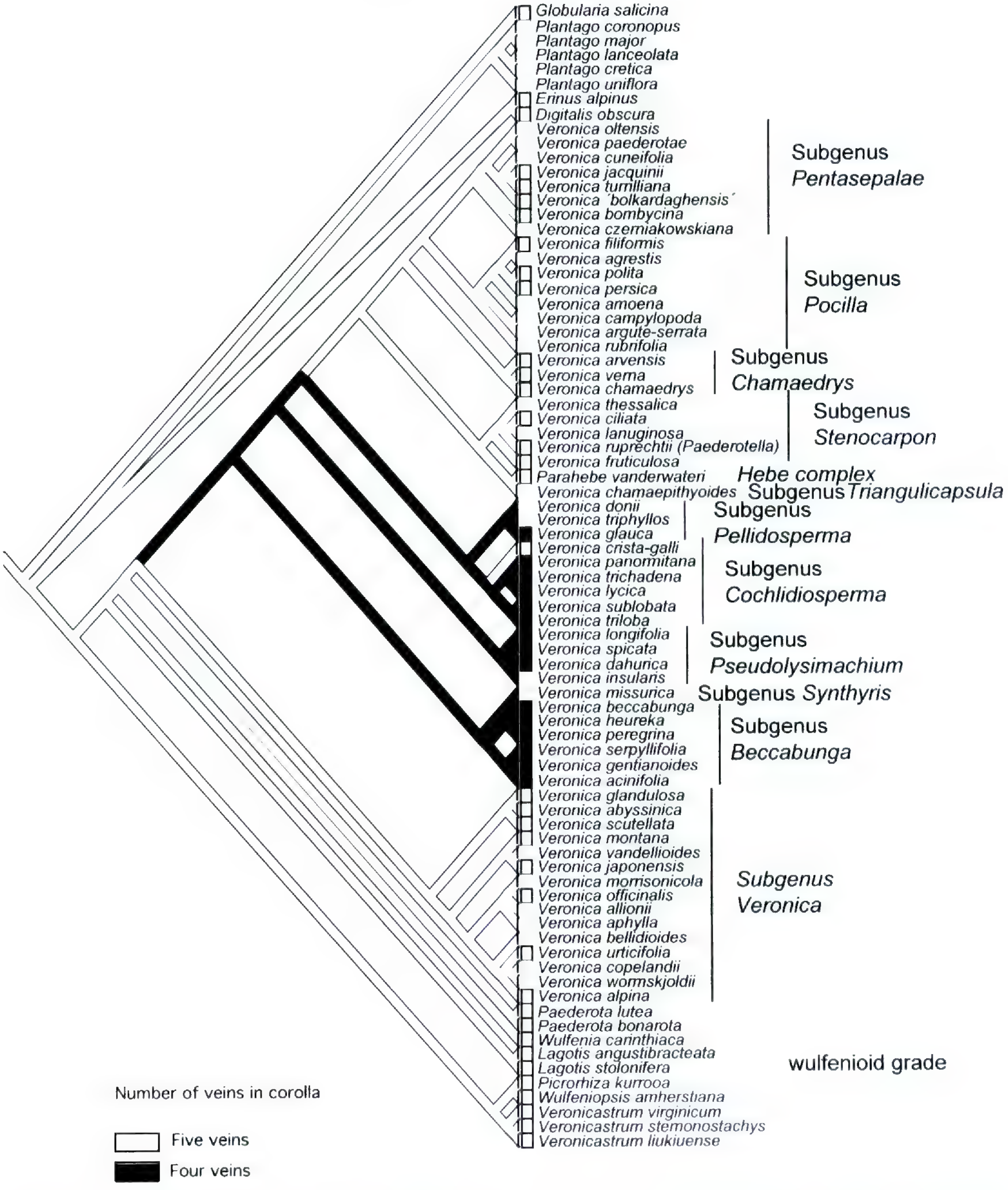

Figure 7. Occurrence of four and five corolla veins mapped on one most parsimonious tree from the combined analysis (ACCTRAN optimization). Only species names with character state boxes in front of the name have been studied. *Veronica* "*bolkardaghensis*" is an abbreviation for *Veronica bombycina* subsp. *bolkardaghensis*.

Hebe. However, the re-emergence of the second midrib in the posterior corolla lobe after it has been lost once seems unlikely. Therefore, the possibility of a parallel evolutionary shift to a single midrib should be considered. Further analyses on the vascular pattern in species not investigated so far and on the correlation of the fifth calyx lobe and the lack of fusion in midribs would be worthwhile.

Flower size is also not a phylogenetically stable character, with size varying considerably between closely related species. For example, *Veronica verna* and *V. chamaedrys*, *V. triphyllos* and *V. donii* or *V. panormitana*/*V. trichadena* and *V. lycica* are sister pairs in our analysis (Figs. 1–5) that differ grossly in flower size, with the first in these pairs having a minute flower and the second having a

flower three to four times the size. Reduction in flower size is probably in all these cases due to a shift to a selfing breeding system.

Flower color is often not even stable within species. Flowers are mostly variations of white, pink, purple, or blue with the exceptions of *Paederota lutea*, *Lagotis integra*, *Veronicastrum brunonianum*, and *V. formosanum*, which have yellow corollas. Additionally, flower color is often variable within a species, with a tendency for alpine varieties to have darker blue corollas. Blue flowers are warmer than white flowers (Savile, 1972) and are therefore more attractive for pollinators.

PALYNOLOGY

Pollen offers a variety of characters that have been used for taxonomic purposes in Veroniceae. Hong (1984) intensively studied pollen morphology within Veroniceae and recognized eight different types. By comparing his results with our phylogenetic hypothesis, some evolutionary trends of pollen grain characters can be revealed. The type of pollen of *Plantago* and *Aragoa* is completely different from that of *Digitalis* and Veroniceae and is therefore an autapomorphy (Bello et al., 2002). *Digitalis* has three-colporate, isopolar-spheroid pollen with a wide colpus and microreticulate tectum (Minkin & Eshbaugh, 1989). This type of pollen resembles that of Hong's *Paederota* type, which occurs in *Paederota*, *Wulfenia*, *Lagotis*, *Picrorhiza scrophulariiflora*, and subgenus *Pseudolysimachium* of *Veronica* (Hong, 1984; Argue, 1995). It is inferred to be ancestral in Veroniceae (result not shown) and plesiomorphic in Scrophulariaceae (Argue, 1995). From this, we can infer the derivation of Hong's *Scrofella* type in *Scrofella*, *Veronicastrum*, and *Picrorhiza kurrooa* and his *Wulfeniopsis* type in *Wulfeniopsis* by assuming a narrowing of the colpus, elongation of the os (indistinct in *Wulfeniopsis*), and perforation and smoothing of the tectum. The first two characters may be correlated with the decrease in size (especially a narrowing from a spheroid form to a prolate form) in these two types. Apparently the *Scrofella* type evolved twice in *Veronicastrum* and *Picrorhiza kurrooa* or the *Paederota* type re-evolved in *P. scrophulariiflora*. However, we should be careful with this inference, because relationships in the wulfenioid grade are only weakly supported. Assuming the relationships in the ITS analysis (Fig. 1) are correct, as supported by Bayesian maximum likelihood analysis of the combined data set (Fig. 5), would require an independent origin of the *Scrofella* type pollen in *Veronicastrum* and the *Picrorhiza–Wulfeniopsis* clade.

The distinction between these three types and the remaining five types coincides with the distinction between *Veronica* s.l. and the wulfenioid grade. It is marked by the change from a three-colporate to three-colpate pollen. The function of pores in the colpi is unclear, but their loss may be associated with prevention of water loss. Other differences include the microreticulate tectum in the *Paederota* type versus a striate-reticulate tectum in *Veronica*. Exceptions to this distinction are *V. javanica*, *V. oligosperma* (Huang, 1972), and subgenus *Pseudolysimachium*, which have *Paederota* type pollen (Hong, 1984). *Veronica schmidtiana* from subgenus *Pseudolysimachium* constitutes an exception from the exception with having *Veronica* type pollen (Hong, 1984). Thus, the three-colporate pollen in *Pseudolysimachium* may be a reversal. More detailed investigation of relationships and pollen evolution within this group is necessary. Hong (1984) recognized two main types among species of *Veronica*, his *Veronica* and *Stenocarpon* types. However, he noticed intermediate species between these two similar types, which was later confirmed by a more detailed analysis (Martínez-Ortega et al., 2000). They suggested multiple origins of Hong's *Stenocarpon* type (with tectum neither typically micror nor typically striate-reticulate) from his *Veronica* type (with striate-reticulate tectum), which is supported by a comparison with our phylogenetic hypothesis (result not shown). Within *Veronica*, Martínez-Ortega et al. (2000: 27) found "the value of pollen characters as taxonomic tools. . .restricted to a small number of cases and does not seem very remarkable." One of these cases is the clade of subgenera *Pellidosperma* and *Cochlidiosperma*, which share a perforate tectum, a narrow colpus with jagged margins, and a more oblate shape (Hong, 1984; Fernández & Pastor, 1997). Within this group, pollen of *V. crista-galli* is differentiated by an irregularly rugulose tectum, whereas the remainder of the subgenus has supratectal spinules (Hong, 1984). The pollen of *V. crista-galli* is thought to be a specialized form of the *Stenocarpon* type, whereas the pollen of subgenus *Cochlidiosperma* does not resemble any other *Veronica* pollen (Hong & Nilsson, 1983; Hong, 1984). Based on these differences in pollen, together with smaller differences in other characters, Hong and Nilsson (1983) re-erected the genus *Cochlidiosperma* (Rchb.) Rchb. for subgenus *Cochlidiosperma* without *V. crista-galli* and *Diplophyllum* for *V. crista-galli* and *V. simensis*. The last pollen type recognized by Hong (1984) is represented by *Detzneria tubata* only, a species divergent in many respects, including having larger pollen with oblong lumina,

a smooth colpus membrane, and a macroreticulate tectum (Hong, 1984).

CAPSULE

According to Hong (1984), capsules of *Veronica* are characteristically laterally compressed and two-lobed in contrast to the turgid, apically tapered capsules of the wulfenioid grade. He outlined a simple progression from turgid and apically tapered capsules via the apically tapered but compressed capsules (e.g., *V. eriogyne*) to the increasingly compressed and two-lobed capsules. This hypothesis is one of the reasons why cladograms by Hong (1984) and Kampny and Dengler (1997) show a sister-group relationship of the Hebe complex and other subclades of *Veronica*. This simple evolutionary trend is not compatible with our hypothesis based on DNA sequence data (comparison not shown). Compressed, wide capsules are probably synapomorphic for *Veronica* s.l., but then several different trends occurred. Specializations led to loss of half the capsule, megaspermy (all species of subg. *Cochlidiosperma*), and globose capsules in subgenus *Cochlidiosperma* (all species except *V. cristagalli*). Flabellate or rhombic capsules evolved in the series *Canae* of subgenus *Veronica*, and obdeltate capsules in subgenus *Triangulicapsula*. The separation of the two capsule halves is taken to the extreme in the relationship of *V. biloba*. In subgenus *Pseudolysimachium*, capsules either retained an ancestrally thicker capsule or regained the ovoid capsule. Tendencies to a longer and less wide capsule, which is correlated with a less emarginate and two-lobed condition, occurred in parallel in the Officinalis–Alpina group of subgenus *Veronica* and in *V. anagallis-V. aquatica* and relatives. The greatest diversity in capsule shape is found in subgenus *Stenocarpon*. Here, capsule shape varies from cordate (*V. thessalica, V. saturejoides*), to suborbicular to widely elliptic (*V. fruticulosa, V. mampodrensis*), to orbicular (*V. ruprechtii*), to oblong-lanceolate (*V. fruticans, V. ciliata*). The fruit apex correspondingly varies between notched, obtuse, and acute.

Within the Hebe complex, capsule flattening was used to differentiate *Parahebe* species with laterally compressed, apically notched capsules from *Hebe* species with dorsiventrally compressed, apically tapered capsules (van Royen, 1972). However, the clear distinction did not hold in New Zealand, although DNA sequence analysis showed that those species of subgenus *Hebe* with laterally compressed capsules (e.g., *Hebe* "Semiflagriformes" and "Grandiflorae"; Moore & Ashwin in Allan, 1961) fall into the grade at the base of the main *Hebe* clade together with species of "Parahebe" (Wagstaff & Garnock-Jones, 1998). We can, therefore, be sure that the ancestor of the Hebe complex had a laterally compressed capsule, and the dorsiventrally compressed capsule probably arose only once.

Capsule dehiscence is an important character in Veroniceae, representing important steps in their evolution. The combination of a septicidal and loculicidal dehiscence is a synapomorphy for the tribe because other Scrophulariaceae have mostly septicidal capsules (Kampny & Dengler, 1997). Within *Veronica* s.l., dehiscence is correlated with capsule morphology. In species with cordate capsules, the opening is loculicidal, whereas in species with an apically tapering capsule the opening is generally loculicidal and septicidal. This septicidal opening differs, however, from the usual mode because the median column remains intact, whereas in true septicidal openings the median column is also parted (Römpp, 1928).

Capsule dehiscence used to be cited as diagnostic for *Veronica* s. str., with a loculicidal capsule, and species of the Hebe complex, in which the capsule is pseudo-septicidal and only to some extent loculicidal (e.g., van Royen, 1972). However, several *Veronica* species, such as *V. javanica, V. fruticulosa*, subgenus *Beccabunga*, subgenus *Pseudolysimachium*, and some species of subgenus *Pentasepalae* also are partly pseudo-septicidal by means of a median fissure (Römpp, 1928) to semi-septicidal with an apical rupture of the placentar column (MMO, pers. obs.).

EMBRYOLOGY

Endosperm formation, especially the formation of chalazal and micropylar endosperm haustoria, were studied by Gscheidle (1924), Weiß (1932), Glisic (1937), Yamazaki (1957), and Afanasiyeva (1971). Glisic (1937) gave a first phylogenetic scheme for the evolution of the endosperm in Veroniceae, which is shown in Figure 8. The only members of Veroniceae outside *Veronica* s.l. that have been studied are *Wulfenia* and *Veronicastrum* (Gscheidle, 1924; Weiß, 1932; Yamazaki, 1957). Both are characterized by a uninucleate four-celled chalazal and a uninucleate four-celled (later a four-nucleate one-celled) micropylar haustorium (Weiß, 1932; Yamazaki, 1957; *Veronica* I sensu Glisic, 1937, Fig. 8). Species of subgenus *Pseudolysimachium* have the same type of endosperm formation, which is believed to be primitive in Veroniceae (Weiß, 1932; Glisic, 1937; Yamazaki, 1957, *Veronica* II sensu Glisic, Fig. 8) and occurs outside Veroniceae in *Erinus* and *Digitalis* (Glisic, 1937; Hartl, 1966).

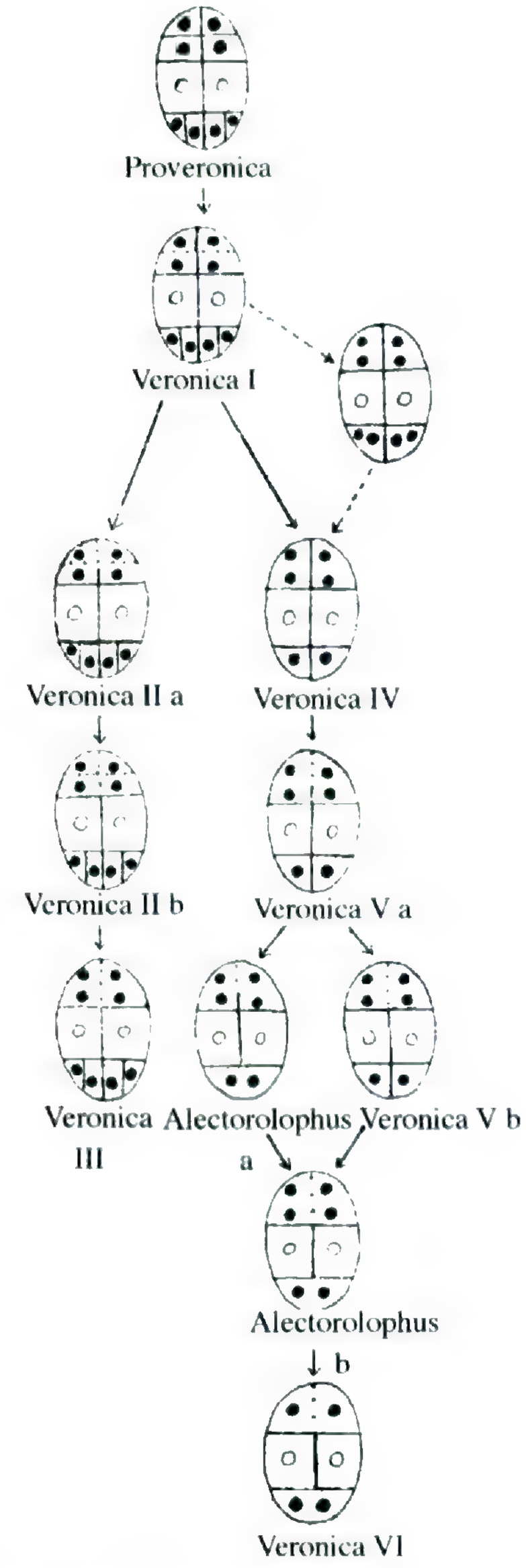

Figure 8. Phylogenetic scheme of endosperm evolution in *Veronica*, modified from Glisic (1937). The chalazal region is on the top of the embryo, the micropylar region on the bottom.

Glisic's scheme (1937, Fig. 8) fits nicely with our molecular hypothesis in showing a trend of reduction from the primitive type discussed above to an intermediate type that differs in having only a two-celled chalazal and a binucleate two-celled micropylar haustorium. It can be found in species of the Alpina and Officinalis groups in subgenus *Veronica* (Gscheidle, 1924; Weiß, 1932; Yamazaki, 1957; Afanasiyeva, 1971; *Veronica* IV, V sensu Glisic, 1937, Fig. 8). It can also be found in *V. scutellata*, *V. fruticulosa*, and *V. austriaca* (Afanasiyeva, 1971). The latter result is surprising and needs confirmation, because all related species show a different endosperm development (see below). The African group of subgenus *Veronica* has not been studied yet. Two other species from subgenus *Veronica*, *V. montana* (Afanasiyeva, 1971) and *V. miqueliana* (Yamazaki, 1957), differ from the previous species in having only one cell in the chalazal haustorium, which is, however, binucleate. This is the chalazal haustorium type found in most species of *Veronica* (incl. *Hebe*; Gscheidle, 1924; Weiß, 1932; Yamazaki, 1957; Afanasiyeva, 1971, Alectorolophus-type sensu Glisic, 1937, Fig. 8). Chalazal haustoria from species of the subgenera *Pentasepalae* and *Chamaedrys* share the distinctive feature of a lateral appendage (Weiß, 1932; Yamazaki, 1957). This appendage was also found in *V. persica* by Yamazaki (1957) but not by Gscheidle (1924) and Weiß (1932). The micropylar haustorium also experiences a reduction in some taxa. In species from subgenus *Cochlidiosperma* (but not *V. crista-galli*) and *V. miqueliana* the micropylar haustorium consists of two uninucleate cells in contrast to the two binucleate cells in other species of *Veronica* (Yamazaki, 1957; Afanasiyeva, 1971, *Veronica* VI sensu Glisic, 1937, Fig. 8). Other than this reduction in nuclei number, the micropylar haustorium is variable in overall shape but lacks diagnostic characters for the distinction of different types over the whole genus (Gscheidle, 1924; Weiß, 1932). Variations characterizing smaller groups of species are, however, possible, such as the more aggressively invading haustorium of the Beccabunga group (including *V. peregrina*) in comparison with the Serpyllifolia group. Thus, endosperm development in *Veronica* shows an increasing reduction in number of cells and nuclei, which is more primitive and labile in the first-branching clades of *Veronica* and becomes more canalized subsequently and leads to the most reduced stage in subgenus *Cochlidiosperma*.

CHROMOSOME NUMBER

Chromosome numbers are available for many species of the Veroniceae. By mapping chromosome numbers on our phylogenetic tree (results not shown) we can infer some trends regarding the karyological evolution. However, no answer can be given to the question about the ancestral number of chromosomes. Lepper (1964) hypothesized an ancestral number of $x = 5$ followed by a polyploid event and subsequent reductions. Outgroup comparison is inconclusive, with three different base numbers found in our outgroups, $x = 8$ in *Globularia*, $x = 7$ in *Digitalis* and *Erinus*, and $x = 6$ as the ancestral base number of *Plantago* hypothe-

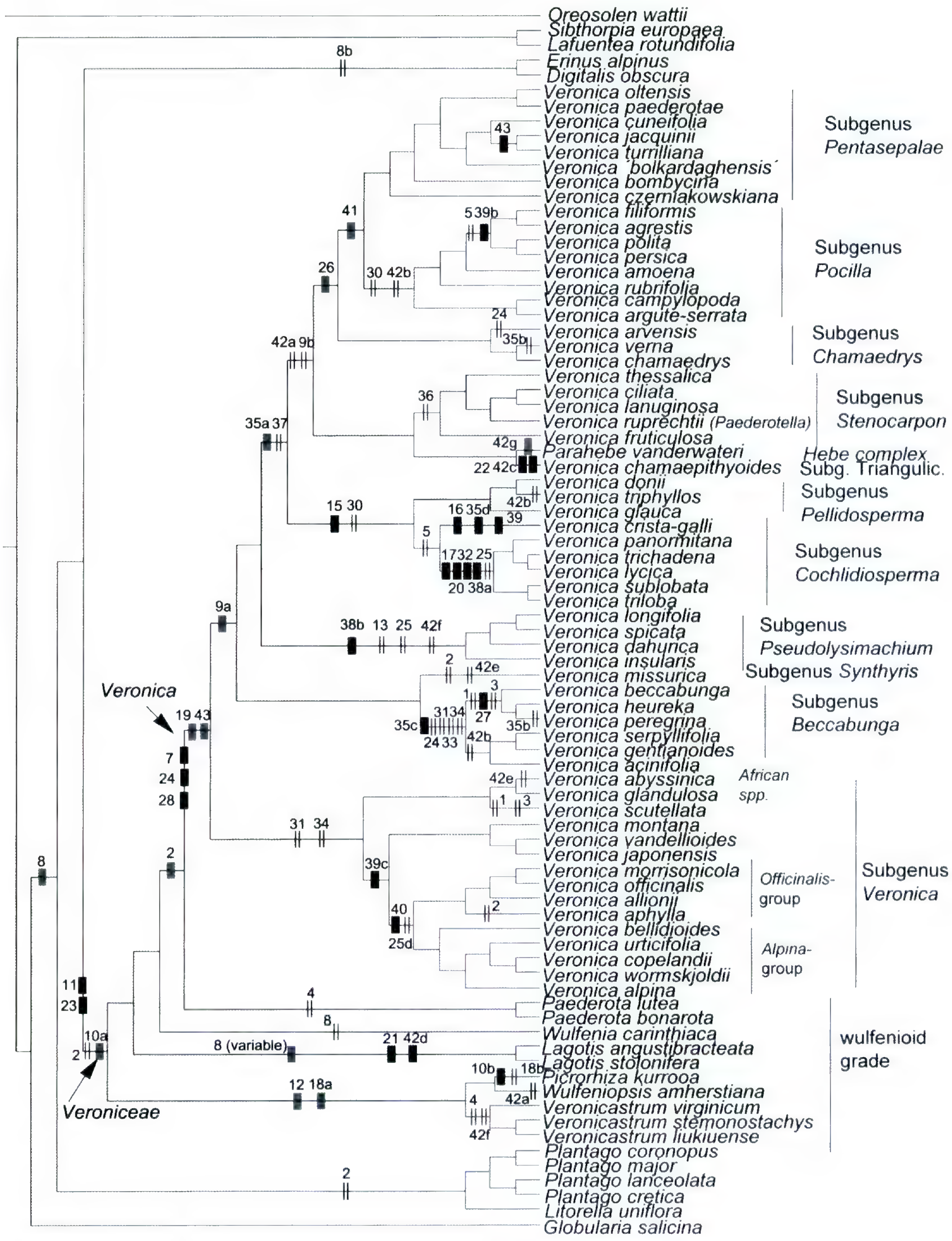

Figure 9. Structural, ecological, and phytochemical synapomorphies as discussed in the text mapped onto one most parsimonious tree from the combined analysis. Parallel bars refer to parallelisms, gray boxes to synapomorphies with reversals, and black boxes to synapomorphies without reversals. The numbers match those in Table 2.

Table 2. Characters of Veroniceae and their states that are possible synapomorphies for various taxa in the tribe. See Figure 9 for details of their distribution.

Character #	Character	Derived character state
1	habitat	aquatic habitat (see Albach, 2002)
2	growth form	basal rosette
3	indumentum	loss of eglandular hairs (see Albach, 2002)
4	hair type	branched hairs (see Albach, 2002)
5	flower organization	solitary flowers
6	flower development	stamen initiation simultaneously or before corolla initiation
7	calyx	calyx lobe reduction to four; if five, last sepal formed after corolla
8	corolla	a—tetramerous corolla
		b—pentamerous corolla
9	corolla venation	a—four petal veins
		b—five petal veins
10	androecium	a—two stamina
		b—four stamina (see Albach, 2002)
11	androecium	ridged anther cells (see Kampny & Dengler, 1997)
12	pollen structure	narrowing of the colpus, elongation of the os (indistinct in *Wulfeniopsis*), smoothing of tectum
13	pollen structure	a—three-colpate pollen
		b—three-colporate pollen
14	pollen structure	striate-reticulate pollen
15	pollen structure	perforate tectum, narrow colpus with jagged margin
16	pollen structure	rugulose tectum
17	pollen structure	supratectual spinules
18	stigma	a—reduced stigma
		b—no reduced stigma (see Albach, 2002)
19	fruit morphology	laterally compressed capsule
20	fruit morphology	globose capsules
21	gynoecium	reduction of ovule number per locule to one
22	fruit morphology	triangular capsules
23	fruit morphology	septicidal and loculicidal capsule opening
24	seed dispersal	hygrochasy (see Albach, 2002)
25	embryology	a—four-celled haustoria
		b—one- or two-celled haustoria
		c—uni-nucleate two-celled micropylar haustorium
		d—two-celled chalazal haustorium
26	embryology	lateral haustorium appendage
27	embryology	aggressive endosperm haustorium
28	gynoecium	anatropous ovule (see Albach, 2002)
29	seed morphology	flattened seeds (see Albach, 2002)
30	seed morphology	cyathiform seeds (see Albach, 2002)
31	seed morphology	seeds flatter than 0.2 mm (see Albach, 2002)
32	seed morphology	cohlidiospermous seeds, larger than 2 mm (see Albach, 2002)
33	seed morphology	seeds less than 0.02 mg (see Albach, 2002)
34	seed number	more than 30 seeds per capsule (see Albach, 2002)
35	seed ultrastructure	a—verrucate seed coat
		b—colliculate seed coat
		c—reticulate-corrugate seed coat
		d—alveolate seed coat (see Albach, 2002)
36	seed ultrastructure	regularly thickened radial walls (see Albach, 2002)
37	seed morphology	endosperm podium with cork plate (see Albach, 2002)
38	seed ultrastructure	a—no seed coat
		b—intermediate layer of integument participates in seed coat (see Albach, 2002)
39	seed ultrastructure	a—corky outer integument layer
		b—papillae on outer integument layer
		c—cellulose lacking in outer integument layer (see Albach, 2002)

Table 2. Continued.

Character #	Character	Derived character state
40	phytochemistry	mussaenoside (see Albach, 2002)
41	phytochemistry	8-OH-flavones (see Albach, 2002)
42	chromosome number	a—$x = 8$ b—$x = 7$ c—$x = 6$ d—$x = 11$ e—$x = 12$ f—$x = 17$ g—$x = 21$
43	protein bodies in the nucleus	a—two types of protein bodies in nucleus b—spindule-like protein body in nucleus (see Albach, 2002)

sized by Rahn (1996). Species of the wulfenioid grade are heterogeneous with respect to their chromosome base number. All species of *Veronicastrum* and *Picrorhiza* have $x = 17$, and $x = 11$ occurs in all species of *Lagotis* studied so far. *Wulfeniopsis* has $x = 8$, whereas *Wulfenia* has $x = 9$ as do many species of *Veronica*, although Lepper (1964) doubted the homology of these chromosome numbers based on differences in chromosome morphology. The result of $x = 9$ as ancestral chromosome number of *Veronica* is in contrast to the hypothesized ancestral base chromosome number $x = 8$ by Lehmann (1940). This latter number has apparently evolved just once in the clade consisting of subgenera *Pentasepalae*, *Stenocarpon*, *Chamaedrys*, *Triangulicapsula*, *Pocilla* plus the Hebe complex. However, chromosome number evolution continued to $x = 7$ in subgenus *Pocilla*, $x = 6$ in subgenus *Triangulicapsula*, and $x = 21$ in the Hebe complex (with subsequent reductions to $x = 19$ and $x = 20$, see Wagstaff & Garnock-Jones, 1998).

Whereas the base chromosome number of $x = 8$ has apparently evolved just once, $x = 7$ has evolved at least three times independently in *Veronica* (Albach & Chase, 2001). A fourth incidence (not included here) would be *V. baumgartenii*, a relative of *V. aphylla* in subgenus *Veronica*. In the first three incidents inferred here, the aneuploid reduction to $x = 7$ is associated with a switch to an annual life history. This kind of aneuploid reduction in chromosome number is also known from other annuals (Stebbins, 1958; Raven, 1979). In subgenus *Pocilla*, all species are annuals and have $x = 7$. In subgenus *Pellidosperma*, the base number reduction evolved after the evolution of the annual life history in *V. triphyllos*, but *V. praecox*, a member of subgenus *Pellidosperma* not sampled here, has the inferred ancestral character state of $x = 9$. In contrast, base number reduction seems to have evolved before the switch to an annual life history in subgenus *Beccabunga*. Two of its three subgroups (the Acinifolia and Serpyllifolia groups) have $x = 7$, whereas the remaining species have $x = 9$. However, only the Acinifolia group consists of annual species.

A reduction in base chromosome number (dysploidy) among annual species relative to their perennial progenitors has been shown in other groups of plants (e.g., *Arabidopsis thaliana*: Koch et al., 1999; Asteraceae: Babcock, 1947; Jackson, 1962; Watanabe et al., 1999; Baldwin et al., 2002; Dipsacaceae: Ehrendorfer, 1965). Reduced chromosome number, however, is only one aspect of annuals to reduce the recombination rate (Ehrendorfer, 1970). Another common trend is the evolution of selfing. Recombination may be a disadvantage in annuals because maintaining successful combinations of genes is more important than in perennials, which can compensate for low hybrid-pollen and -seed fertility by reproducing again in the following year (Stebbins, 1950). Therefore, increased linkage of genes seems favorable in annuals. This linkage seems connected with more temporary habitats (Stebbins, 1958). In line with this argument, those annual *Veronica* species living in the most mesic, stable habitats (subg. *Cochlidiosperma*) retained the high base chromosome number of $x = 9$. The reason for this connection, however, is not completely clear, but it may be due to the fact that smaller population sizes in unstable, ephemeral habitats allow faster fixation of mutations and contain less genetic diversity, which may be advantageous in outbreeding events. A second non-exclusive hypothesis is that recombination as a defense against pathogens is not necessary because of the short life-span and less pathogen pressure in ephemeral and xeric habitats (Watanabe et al., 1999).

The strange chromosome number of *Veronica peregrina*, with $2n = 52$, and its annual habit have

confused many systematists. Our molecular analyses (Albach & Chase, 2001; Figs. 1–5) revealed a position within the Beccabunga group with a base chromosome number of $x = 9$. Therefore, *V. peregrina* seems to be a hexaploid member of this group, which subsequently lost two chromosomes. Supporting this view is the occurrence of two or three particularly large chromosomes in *V. peregrina* (Hofelich, 1935), which may be the result of Robertsonian fusion. Another example of reduced chromosome number after a polyploid event is subgenus *Pseudolysimachium* with $x = 17$. Afanasiyeva and Meshkova (1961) hypothesized an origin from one parent with $x = 8$ and the other with $x = 9$, whereas Graze (1935) assumed an origin from an ancestor with $x = 18$ derived from diploid parents with $x = 9$, based on a larger chromosome in species of subgenus *Pseudolysimachium* with $n = 17$ and two larger chromosomes in those with $n = 34$. Additionally, Graze (1935) reported the occurrence of a variety of *V. longifolia* with 36 chromosomes of equal size. Given the congruent results from both the nuclear genome (Albach & Chase, 2001; Fig. 1) and plastid genome (Albach et al., in press a; Fig. 2) that place subgenus *Pseudolysimachium* among the subgenera with $x = 9$ and distant to subgenera with $x = 8$, Graze's hypothesis seems more plausible.

Conclusion

Veronica is an example of reduction of parts in various characters. As shown for the fifth stamen in Lamiales (Walker-Larsen & Harder, 2000), the reduction of parts is reversible among taxa branching from basal nodes and less so among derived taxa. This indicates increased canalization of characters in these derived taxa in which mutations leading to reversal are becoming less and less probable because of subsequent mutations. The reason the reduction in parts is so common in Veroniceae may be correlation of characters (e.g., Lehmann, 1918). In flowers, adaptation to other pollinators that prefer short and rotate corolla tubes may have necessitated the reduction of many parts, starting a cascade of subsequent mutations in other parts of the flower. The same may be true for the evolution of annual species that experienced parallel reductions in stature and phytochemical arsenal (Albach et al., in press a; Taskova & Albach, in prep.). Parallel evolution makes it difficult to find synapomorphies for all clades. We have mapped those discovered in this study on one of our most parsimonious trees from the combined analysis (Fig. 9 for ecological, structural, and phytochemical characters). Comparison of Figure 3 and Figure 9 shows a general correlation of molecular and structural evolution. Clades well supported by nucleotide characters tend to have more structural synapomorphies. Furthermore, evolutionarily stable characters can be found in every kind of structure and developmental process—seed, embryo, pollen, corolla, and flower development. However, many of these characters are difficult to observe and are therefore not useful to identify subgenera in the field. This study further stresses the need for more information on structural characters to understand the evolution of our study group.

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CLADISTIC RELATIONSHIPS OF *AECHMEA* (BROMELIACEAE, BROMELIOIDEAE) AND ALLIED GENERA[1]

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Abstract

Aechmea (ca. 220 species) is the largest and most diverse genus in Bromelioideae (Bromeliaceae), and several dissimilar generic concepts and infrageneric classifications have been proposed, frequently involving other closely related Bromelioideae. A morphology-based phylogenetic analysis using parsimony was conducted with 86 taxa, including 52 *Aechmea* (7 of the 8 recognized subgenera represented) and 34 exemplars from 9 closely related genera as the ingroup. Two species of *Cryptanthus* were included as the outgroup. The main objectives were to assess the validity of the major infrageneric classification systems proposed for *Aechmea* and to elucidate the phylogenetic position of *Aechmea* and putatively related genera in subfamily Bromelioideae. The topology of the consensus tree suggests that *Acanthostachys*, *Billbergia*, *Portea*, and non-Brazilian *Ronnbergia* may be monophyletic. *Hohenbergia*, *Streptocalyx*, and *Quesnelia* are paraphyletic or polyphyletic, as are most subgenera of *Aechmea*, except for subgenera *Chevaliera* and *Macrochordion*, which appear monophyletic. Characters traditionally emphasized in classifications of Bromelioideae displayed high levels of homoplasy, and this may be a reason for the artificiality of the taxonomic systems proposed for these taxa. Due to weak internal support, we refrain from recognizing any new taxonomic rearrangements. These results do provide new insights into the relationships within a number of Bromelioideae genera and suggest directions for future studies.

Key words: *Aechmea*, Bromeliaceae, Bromelioideae, morphology, phylogeny.

In the most recent monograph for Bromeliaceae Smith and Downs (1974, 1977, 1979) placed 2110 species in 48 genera and 3 subfamilies: Pitcairnioideae (740 spp., 15 genera), Tillandsioideae (806 spp., 6 genera), and Bromelioideae (564 spp., 27 genera). During the past 20 years nearly 1160 additional species have been described, increasing the family by half to ca. 3270 species and 56 genera (Luther & Sieff, 1994, 1997; Luther, 2000, 2001).

Aechmea Ruiz & Pav. (ca. 220 species; Luther, 2000) is the largest and most diverse genus in Bromelioideae with a distribution throughout tropical America. Nearly 70% of *Aechmea* species (Smith & Downs, 1979; Luther & Sieff, 1994, 1997; Luther, 2001) are distributed in Brazil, and the Atlantic Rain Forest is the center of diversity for *Aechmea* as well as for most genera of the subfamily (Smith, 1934). The taxonomic boundaries that separate *Aechmea* from other Bromelioideae genera are vague and in need of revision. This was noted by early taxonomists (Baker, 1879, 1889; Mez, 1892, 1896, 1935) and remains true in the last revision (Smith & Downs, 1979), where some species of *Ronnbergia* E. Morren & André, *Quesnelia* Gaudich., and *Streptocalyx* Beer appear within identification keys for *Aechmea*. According to the conceptual limit of *Aechmea* (sensu Smith & Downs, 1979) species placement often seems arbitrary with several species from other genera easily placed within *Aechmea* and vice versa. Such examples include the transfer of all *Streptocalyx* species into *Aechmea* (Smith & Spencer, 1992), as well as the transfer of species traditionally treated in *Aechmea* to other genera, e.g., *Lymania* Read (1984) and *Ursulaea* Read & Baensch (1994). Smith and Downs (1979) divided *Aechmea* into eight subgenera: *Aechmea*, *Podaechmea* Mez, *Platyaechmea* (Baker) Bak-

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er, *Ortgiesia* (Regel) Mez, *Pothuava* (Baker) Baker, *Lamprococcus* (Beer) Baker, *Macrochordion* (de Vriese) Baker, and *Chevaliera* (Gaudich. ex Beer) Baker, and later Smith and Kress (1989, 1990) elevated or resurrected all of them to generic level. However, the taxonomic changes proposed by Smith and Kress (1989, 1990) were not followed by other authors (Luther & Sieff, 1994; Wendt, 1997; Luther, 2000).

In *Aechmea* two reasons emerge for discordant classifications. First, monographers have stressed only a few characters, and those characters differ from author to author. Second, this problem is amplified by the limited knowledge of many potentially useful diagnostic characters. For example, the intracalyx floral morphology is either poorly preserved or not preserved at all in herbarium collections and therefore remains scantily understood. Consequently, past monographs relied heavily on vegetative, inflorescence, sepal, and floral bract features that are observed on herbarium specimens. The importance of fresh or liquid-preserved material for morphological analysis of reproductive structures has been stressed (Utley, 1983; Brown & Gilmartin, 1984; Leme, 2000).

Recent advances in the systematics of Bromeliaceae have been realized using cladistic analyses of molecular and morphological data. These works have addressed phylogenetic relationships between the subfamilies (Ranker et al., 1990; Terry et al., 1997; Horres et al., 2000) and genera of Tillandsioideae (Gilmartin & Brown, 1986; Terry & Brown, 1997) and Pitcairnioideae (Varadarajan & Gilmartin, 1988). The monophyly of Bromelioideae is well supported by cladistic analysis based on morphological and molecular data (Ranker et al., 1990; Terry et al., 1997; Horres et al., 2000). However, at a generic level, except for work by Ramírez (1996) that used morphological characters to explore the sister taxon relationships and the putative monophyletic status for *Cryptanthus* Otto & A. Dietr., and by Brown and Leme (2000) that presented a cladistic analysis of *Nidularium* Lem. and related Bromelioideae genera (*Wittrockia* Lindm., *Neoregelia* L. B. Sm., *Canistrum* E. Morren, *Canistropsis* Mez (Leme), *Edmundoa* Leme), there is no known cladistic study within Bromelioideae involving the taxa analyzed in this work (i.e., *Aechmea* and related genera).

The main objectives of this paper were to investigate the phylogenetic position of *Aechmea* and other related genera of Bromelioideae, and to assess the validity of past infrageneric classifications proposed for *Aechmea* (Baker, 1889; Mez, 1892, 1896, 1935; Smith & Downs, 1979; Smith & Kress, 1989, 1990; Smith & Spencer, 1992). We also hope to improve knowledge of Bromelioideae morphology by including underutilized and new character data.

Materials and Methods

Taxon Sampling

A total of 86 taxa (83 species and 3 varieties) representing 7 of the 8 subgenera of *Aechmea* (50 spp., 2 var.), as well as the genera *Acanthostachys* Klotzsch (2 spp.), *Billbergia* Thunb. (6 spp.), *Fernseea* Baker (1 sp.), *Lymania* (1 sp.), *Hohenbergia* Schult. f. (5 spp.), *Portea* Brongn. ex Koch (4 spp.), *Quesnelia* (9 spp., 1 var.), *Ronnbergia* (2 spp.), and *Streptocalyx* (3 spp.), were sampled as ingroups (Table 1). These latter genera were selected because they have a clear morphological affinity to *Aechmea* and are themselves weakly delimited. Species were sampled to include as much as possible the known morphological and geographic variation of each genus or subgenus analyzed. Specimens were collected in the field or obtained from living collections in Brazil. For those cultivated samples listed in Table 1, horticultural cultivars and hybrids were avoided, using only specimens previously collected from the wild. Exemplar specimens (one or two specimens per species or variety) were used for the scoring of character states. In 75% of the genera and subgenera sampled it was possible to include the type species. Voucher specimens are listed in Table 1, and a summary of the representative percentage for each taxon sampled is presented in Table 2.

Two species from the genus *Cryptanthus* were selected as the outgroup on the basis of recent molecular work (Terry et al., 1997) that placed *Cryptanthus* in a basal position relative to those ingroup genera analyzed here.

Morphological Data

A total of 60 characters were coded, including 13 vegetative, 46 reproductive, and 1 pollen character. The characters and their states used in this analysis are presented in Appendix 1. For 79 taxa (including the outgroup), all floral characters and some leaf characters such as ornamentation and number were scored from living plants or flowers preserved in 70% alcohol. The remaining characters were determined after preparing the herbarium voucher. For 7 species (*Aechmea allenii, A. drakeana, A. fraseri, A. involucrata, A. mariae-reginae, Ronnbergia deleonii,* and *R. morreniana*), all morphological data were obtained from herbarium specimens (SEL), complemented with photos of liv-

Table 1. Taxa used in the phylogenetic analysis. Type species of genera and subgenera are indicated in bold. Subgeneric assignments correspond to the traditional classification of Bromelioideae, sensu Smith and Downs (1979). Voucher information includes collector with number, and herbarium code. * Indicates plants collected from cultivation.

Taxon	Geographic origin	Voucher
Acanthostachys Klotzsch		
A. pitcairnioides (Mez) Rauh & Barthlott	Brazil, Bahia*	*Faria 03* (RFA)
***A strobilacea* (Schult. f.) Klotzsch**	Eastern Brazil*	*Faria 02* (RFA)
	Brazil, Paraná	*Hatschbach 12933* (RFA)
Aechmea subg. *Aechmea* Ruiz & Pav.		
A. angustifolia Poepp. & Endl.	Costa Rica*	*Wendt 346* (RFA)
A. aquilega (Salisb.) Griseb.	Brazil, Paraíba*	*Vieira 1249* (RFA)
A. blanchetiana (Baker) L. B. Sm.	Brazil, Bahia*	*Faria 13* (RFA)
A. correia-araujoi E. Pereira & Moutinho	Brazil, Bahia*	*Vieira 1247* (RFA)
A. eurycorymbus Harms	Brazil, Pernambuco*	*Vieira 1250* (RFA)
	Brazil, Pernambuco*	*Faria 14* (RFA)
A. fosteriana L. B. Sm.	Brazil, Espírito Santo*	*Vieira 1217* (RFA)
	Brazil, Espírito Santo*	*Faria 34* (RFA)
A. gurkeniana E. Pereira & Moutinho	Brazil, Bahia*	*Vieira 1212* (RFA)
	Brazil, Bahia*	*Faria 33* (RFA)
A. lingulata (L.) Baker	Brazil, Rio de Janeiro	*Faria 30* (RFA)
A. marauensis Leme	Brazil, Bahia*	*Faria 18* (RFA)
A. mutica L. B. Sm.	Brazil, Espírito Santo*	*Wendt 375* (RFA)
	Brazil, Espírito Santo	*Faria 26* (RFA)
A. orlandiana L. B. Sm.	Brazil, Espírito Santo*	*Vieira 1219* (RFA)
	Brazil, Espírito Santo*	*Faria 32* (RFA)
A. penduliflora André	Costa Rica*	*Vieira 1275* (RFA)
A. purpureorosea (Hook.) Wawra	Brazil, Rio de Janeiro*	*Vieira 1256* (RFA)
A. ramosa var. *festiva* L. B. Sm.	Brazil, Espírito Santo*	*Vieira 1216* (RFA)
	Brazil, Espírito Santo*	*Faria 42* (RFA)
A. ramosa var. *ramosa* Mart. ex Schult. f.	Brazil, Espírito Santo	*Faria 25* (RFA)
A. rubens (L. B. Sm.) L. B. Sm.	Northeast Brazil*	*Faria 21* (RFA)
A. stelligera L. B. Sm.	Northeast Brazil*	*Faria 17* (RFA)
A. werdermannii Harms	Brazil, Pernambuco*	*Faria 16* (RFA)
Aechmea subg. *Chevaliera* (Gaudich. ex Beer) Baker		
A. multiflora L. B. Sm.	Brazil*	*Canela 02* (RFA)
A. saxicola L. B. Sm.	Brazil, Espírito Santo	*Faria 27* (RFA)
***A. sphaerocephala* Baker**	Brazil, Rio de Janeiro	*Wendt 330* (RFA)
Aechmea subg. *Lamprococcus* (Beer) Baker		
A. fulgens Brongn.	Brazil, Bahia*	*Vieira 1252* (RFA)
A. miniata (Beer) hort. ex Baker	Brazil, Bahia*	*Vieira 1259* (RFA)
A. warasii E. Pereira	Brazil, Espírito Santo*	*Vieira 1267* (RFA)
A. weilbachii var. *albipetala* Leme & A. Costa	Brazil, Rio de Janeiro*	*Costa s.n.* (R)
A. weilbachii var. *weilbachii* Didrichsen	Brazil, Rio de Janeiro*	*Vieira 1208* (RFA)
Aechmea subg. *Macrochordion* (de Vriese) Baker		
***A. bromeliifolia* (Rudge) Baker**	Brazil, Espírito Santo*	*Faria 39* (RFA)
A. triangularis L. B. Sm.	Brazil, Espírito Santo	*Wendt 392* (RFA)
Aechmea subg. *Ortgiesia* (Regel) Mez		
A. burle-marxii E. Pereira	Brazil, Bahia*	*Wendt 339* (RFA)
A. calyculata (E. Morren) Baker	Brazil, Santa Catarina*	*Vieira 1221* (RFA)
A. coelestis (K. Koch) E. Morren	Brazil, Espírito Santo	*Ramaldes 16* (RFA)
A. gamosepala Wittm.	Southern Brazil*	*Wendt 351* (RFA)
***A. recurvata* (Klotzsch) L. B. Sm.**	Southern Brazil*	*Faria 31* (RFA)
	Southern Brazil*	*Faria 45* (RFA)

Table 1. Continued.

Taxon	Geographic origin	Voucher
Aechmea subg. *Platyaechmea* (Baker) Baker		
A. caesia E. Morren ex Baker	Brazil, Rio de Janeiro*	*Vieira 1211* (RFA)
A. chantinii (Carrière) Baker	Brazil, Amazonas*	*Wendt 340* (RFA)
A. dealbata E. Morren ex Baker	Brazil, Rio de Janeiro*	*Faria 37* (RFA)
***A. distichantha* Lem.**	Brazil, São Paulo*	*Faria 10* (RFA)
A. fasciata (Lindl.) Baker	Brazil, Rio de Janeiro*	*Vieira 1246* (RFA)
Aechmea subg. *Pothuava* (Baker) Baker		
A. allenii L. B. Sm.	Panamá	*Luther s.n.* (SEL)
A. alopecurus Mez	Brazil, Bahia*	*Faria 07* (RFA)
A. bocainensis E. Pereira & Leme	Brazil, São Paulo*	*Gurken s.n.* (RFA)
A. brueggeri Leme	Brazil, Minas Gerais*	*Faria 05* (RFA)
A. drakeana André	Ecuador	*Girko E90-195J* (SEL)
A. fraseri Baker	Ecuador	*Kessler 2414* (SEL)
	Ecuador	*Luther s.n.* (SEL)
A. guarapariensis E. Pereira & Leme	Brazil, Espírito Santo*	*Wendt 349* (RFA)
A. involucrata André	Ecuador	*Berg s.n.* (SEL)
	Ecuador	*Cathcart s.n.* (SEL)
A. mariae-reginae H. Wendl.	Costa Rica	*Meerow s.n.* (SEL)
***A. nudicaulis* (L.) Griseb.**	Brazil, Rio de Janeiro	*Sampaio s.n.* (RFA)
A. ornata Baker	Brazil, Paraná	*Wendt 290* (RFA)
	Brazil, Rio de Janeiro	*Wendt 365* (RFA)
A. pectinata Baker	Brazil, Rio de Janeiro	*Wendt 334* (RFA)
A. pineliana (Brongn. ex Planch.) Baker	Brazil, Espírito Santo*	*Vieira 1213* (RFA)
	Brazil, Rio de Janeiro*	*Faria 40* (RFA)
A. vanhoutteana (Van Houtte) Mez	Brazil, Rio de Janeiro	*Ribeiro s.n.* (RFA)
	Brazil, Rio de Janeiro	*Wendt 372* (RFA)
Billbergia subg. *Billbergia* Thunb.		
***B. amoena* (Lodd.) Lindl.**	Eastern Brazil*	*Faria 08* (RFA)
B. distachia (Vell.) Mez	Southern Brazil*	*Faria 06 (RFA)*
B. elegans Mart. ex Schult. f.	Brazil, Espírito Santo*	*Costa 545* (RFA)
B. euphemiae E. Morren	Brazil, Espírito Santo	*Wendt 388* (RFA)
B. pyramidalis (Sims) Lindl.	Brazil, Rio de Janeiro	*Wendt 360* (RFA)
	Brazil, Rio de Janeiro	*Faria 28* (RFA)
B. sanderiana E. Morren	Brazil, Espírito Santo	*Wendt 389* (RFA)
Cryptanthus Otto & A. Dietr.		
***C. bromelioides* Otto & A. Dietr.**	Brazil, Rio de Janeiro	*Roças s.n.* (RFA)
C. pickelii L. B. Sm.	Brazil, Pernambuco*	*Faria 38* (RFA)
Fernseea Baker		
***F. itatiaiae* (Wawra) Baker**	Brazil, Rio de Janeiro	*Ribeiro 291* (RFA)
Hohenbergia subg. *Hohenbergia* Schult. f.		
H. catingae Ule	Brazil, Bahia*	*Wendt 352* (RFA)
H. correia-araujoi E. Pereira & Moutinho	Brazil, Bahia*	*Vieira 1254* (RFA)
	Brazil, Bahia*	*Wendt 344* (RFA)
H. disjuncta L. B. Sm.	Brazil, Bahia*	*Wendt 336* (RFA)
H. ramageana Mez	Brazil, Bahia	*Pereira 9625* (RFA)
***H. stellata* Schult.f.**	Brazil, Bahia*	*Vieira 1270* (RFA)
Lymania Read		
L. azurea Leme	Brazil, Bahia*	*Faria 44* (RFA)
Portea Brongn. ex K. Koch		
P. alatisepala Philcox	Brazil, Bahia*	*Faria 20* (RFA)
P. fosteriana L. B. Sm.	Brazil, Espírito Santo	*Wendt 396* (RFA)

Table 1. Continued.

Taxon	Geographic origin	Voucher
	Brazil, Espírito Santo	*Wendt 397* (RFA)
P. leptantha Harms	Brazil, Bahia*	*Vieira 1248* (RFA)
	Brazil, Bahia*	*Faria 15* (RFA)
P. petropolitana (Wawra) Mez	Brazil, Rio de Janeiro*	*Faria 09* (RFA)
Quesnelia subg. *Billbergiopsis* Mez		
Q. augusto-coburgii Wawra	Brazil, Rio de Janeiro*	*Vieira 985* (RB)
Q. blanda Mez	Brazil, Rio de Janeiro*	*Vieira s.n.* (RB)
Q. edmundoi var. *edmundoi* L. B. Sm.	Brazil, Rio de Janeiro*	*Vieira 873A* (RB)
Q. edmundoi var. *rubrobracteata* E. Pereira	Brazil, Rio de Janeiro*	*Gurken 1552* (RB)
Q. lateralis Wawra	Brazil, Rio de Janeiro*	*Vieira 1206* (RB)
***Q. liboniana* (De Jonghe) Mez**	Brazil, Rio de Janeiro	*Vieira 1210* (RB)
Q. marmorata (Lem.) Read	Brazil, Rio de Janeiro*	*Faria 01* (RFA)
Q. seideliana L. B. Sm. & Reitz	Brazil, Rio de Janeiro*	*Vieira 968* (RB)
Quesnelia subg. *Quesnelia* Gaudich.		
Q. arvensis (Vell.) Mez	Brazil, Rio de Janeiro	*Vieira 1234* (RB)
***Q. quesneliana* (Brongn.) L. B. Sm.**	Brazil, Rio de Janeiro*	*Gurken 1546* (RB)
	Brazil, Rio de Janeiro*	*Gurken 1543* (RB)
Ronnbergia E. Morren & André		
R. deleonii L. B. Sm.	Ecuador	*Luther s.n.* (SEL)
***R. morreniana* Linden & André**	Ecuador	*Determann s.n.* (SEL)
Streptocalyx Beer		
S. floribundus (Mart. ex Schult. f.) Mez	Brazil, Rio de Janeiro	*Faria 29* (RFA)
S. longifolius (Rudge) Baker	Brazil, Amazonas*	*Vieira 1269* (RFA)
***S. poeppigii* Beer**	Brazil, Amazonas*	*Vieira 1255* (RFA)
	Brazil, Amazonas*	*Wendt 350* (RFA)

ing material. The pollen data were taken from the available literature (Ehler & Schill, 1973; Erdtman & Praglowski, 1974; Wanderley & Melhem, 1991; Halbritter, 1992; Sousa et al., 1997) and scored from herbarium or liquid-preserved samples using the methods described by Wodehouse (1935). Continuous variables (e.g., mature leaf length) were assessed as discrete variables based on observed discontinuous gaps between species.

PHYLOGENETIC ANALYSES

Data were entered into a matrix using the computer program MacClade 4.0 (Maddison & Maddison, 2000), and the phylogenetic analyses were performed with PAUP* 4.0b10 (Swofford, 2001). In the data matrix (Appendix 2), missing character states (0.2%) are indicated with a question mark, and inapplicable character states (3.4%) are indicated with a dash. The large size of this data matrix mandated use of a heuristic search strategy designed to discover islands of most parsimonious trees. These searches were conducted following Olmstead et al. (1993) and Olmstead and Palmer (1994). All characters were unweighted, and multistate characters were treated as unordered. To evaluate the support for each node, 100 bootstrap replicates with full heuristic search were conducted. Relative levels of homoplasy and synapomorphy in the data sets were calculated using the consistency index (CI), the retention index (RI), and the rescaled consistency index (RC) as implemented in PAUP* 4.0b10. Character state changes were mapped on the strict consensus tree using MacClade (Maddison & Maddison, 2000).

RESULTS

The cladistic analysis yielded 158 equally most parsimonious trees of 777 steps length, with 59 informative characters, a consistency index (CI) of 0.142 excluding autapomorphies, a retention index (RI) of 0.606, and a rescaled consistency index (RC) of 0.086. The strict consensus tree is shown in Figure 1. The ingroup is well supported as monophyletic within a bootstrap value of 100% (Fig. 1), but most internal support was less than 50%.

This analysis supports the monophyly of four genera: *Acanthostachys*, *Billbergia*, *Portea*, and *Ronnbergia* and two subgenera of *Aechmea*: *Chev-*

Table 2. Percentage of genera and subgenera sampled for ingroups in this study.

Genus/Subgenus[a]	No. of species[b]	No. of taxa sampled	Percentage sampled[c]
Genus *Acanthostachys* Klotzsch	**2**	**2**	**100%**
Genus *Aechmea* Ruiz & Pav.	**222**	**52**	**23%**
Subgenus *Aechmea* Ruiz & Pav.,	107	18	17%
Subgenus *Chevaliera* (Gaudich. ex Beer) Baker	23	3	13%
Subgenus *Lamprococcus* (Beer) Baker	16	5	31%
Subgenus *Macrochordion* (de Vriese) Baker	11	2	18%
Subgenus *Ortgiesia* (Regel) Mez	21	5	24%
Subgenus *Platyaechmea* (Baker) Baker	18	5	28%
Subgenus *Pothuava* (Baker) Baker	21	14	67%
Subgenus *Podaechmea* Mez	5	0	NA
Genus *Billbergia* Thunb.	**62**	**6**	**10%**
Subgenus *Billbergia* Thunb.	37	6	16%
Subgenus *Helicodea* (Lem.) Baker	25	0	NA
Genus *Fernseea* Baker	**2**	**1**	**50%**
Genus *Hohenbergia* Schult. f.	**50**	**5**	**10%**
Subgenus *Hohenbergia* Schult. f.	30	5	17%
Subgenus *Wittmackiopsis* Mez	20	0	NA
Genus *Lymania* Read	**7**	**1**	**14%**
Genus *Portea* Brongn. ex K. Koch	**9**	**4**	**44%**
Genus *Quesnelia* Gaudich.	**15**	**10**	**56%**
Subgenus *Quesnelia* Gaudich.	2	2	100%
Subgenus *Billbergiopsis* Mez	13	8	62%
Genus *Ronnbergia* E. Morren & André	**11**	**2**	**18%**
Genus *Streptocalyx* Beer	**15**	**3**	**20%**

[a] Classification follows Smith and Downs (1979) except for *Lymania* (Read, 1984) and *Acanthostachys* (Rauh & Barthlott, 1982)
[b] Luther and Sieff (1994, 1997); Luther (2001).
[c] NA = not applicable.

aliera and *Macrochordion* (Fig. 1). Based on our sample, *Hohenbergia* appears paraphyletic, *Lymania* is placed within *Aechmea*, and *Fernseea* is the sister taxon to *Billbergia* (Fig. 1). *Streptocalyx*, *Quesnelia*, and the remaining subgenera of *Aechmea* are polyphyletic (Fig. 1). Most characters analyzed displayed high levels of homoplasy (Table 3). These results support particular elements of some previous classifications, but do not agree closely with any one treatment (Fig. 1). In the consensus tree, nine clades have been identified (Fig. 1).

Discussion

The only generic-level, morphologically based cladistic studies in subfamily Bromelioideae (Brown & Leme, 2000; this study) display two common features. First, consensus trees have notably more resolved nodes than unresolved ones. Second, bootstrap support is lacking (i.e., < 50%) for most of the resolved clades. We have somewhat arbitrarily recognized nine clades that will focus the following discussion.

clade 1

Our results suggest that the genus *Acanthostachys* (Fig. 1) is monophyletic. Smith and Downs (1979) recognized only one species for the genus. The second, *A. pitcairnioides*, was previously treated within *Aechmea* subgenera *Ortgiesia* (Mez, 1896) or *Pothuava* (Smith & Downs, 1979) and later transferred to *Acanthostachys* by Rauh and Barthlott (1982), and our analyses support this treatment. *Acanthostachys strobilacea* and *A. pitcairnioides* differ greatly in flower and inflorescence morphology. Most of the synapomorphies that define the *Acanthostachys* clade are vegetative features (characters 6, filiform leaf blades; 9, long-attenuate leaf apex; 13, scape bracts not imbricate; 34, terminal spine shorter than the floral bract length; 37, concave floral bracts; 60, rosette not forming a water impounding tank). Filiform leaf blades is the only apomorphic character unique for this genus, but this leaf morphology can also be found in species of other bromelioid genera (*Orthophytum* Beer, *Bromelia* L., *Ananas* Mill.), which were not included in this study. Tomlinson (1969) suggested that this

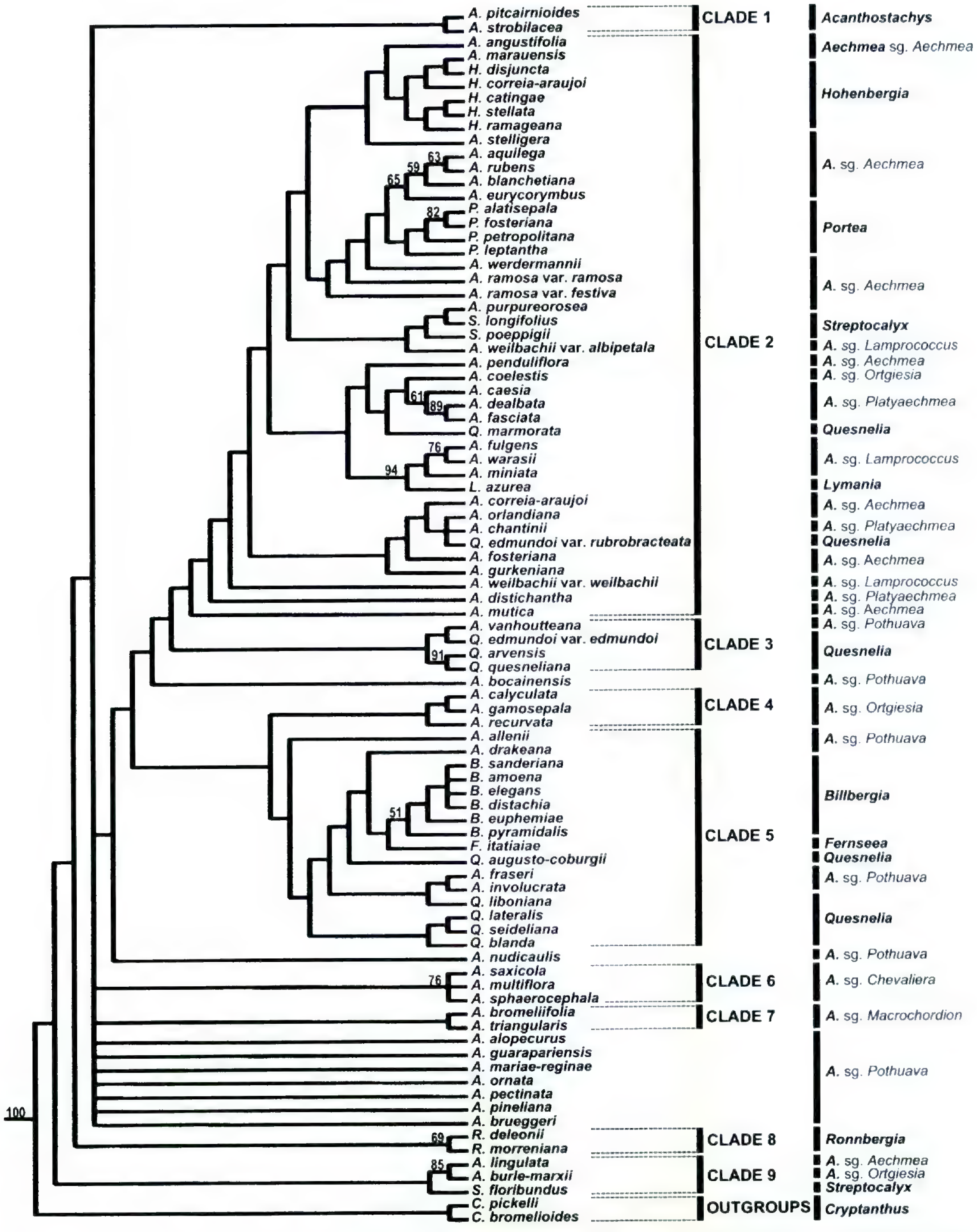

Figure 1. Strict consensus of 158 equally most parsimonious trees of 777 steps for *Aechmea* and related genera produced by cladistic analysis of morphological characters. Genus *Cryptanthus* was used as outgroup. Clades 1 to 9 are discussed in the text. Numbers above branches are the bootstrap percentages (of over 50%). The most recent generic and infrageneric delimitation proposed for subfamily Bromelioideae (Smith & Downs, 1979; Rauh & Barthlott, 1982; Read, 1984) is shown beside the black bars.

Table 3. Number of states, number of steps, and consistency (CI), retention (RI), and rescaled consistency (RC) indices of 60 morphological characters estimated by character diagnostic analysis. Characters are listed according to descending RC values; character numbers refer to those presented in Appendices 1 and 2.

Character	States	Steps	CI	RI	RC
6. Leaf form	3	2	1.00	1.00	1.00
29. Floral bract presence	2	1	1.00	1.00	1.00
56. Filament shape	2	2	0.50	0.86	0.43
54. Ovary surface	3	4	0.50	0.80	0.40
39. Pedicel	2	2	0.50	0.75	0.38
28. Primary bract apex	3	5	0.40	0.93	0.37
24. Primary bract presence	2	3	0.33	0.94	0.32
10. A false midrib	2	2	0.50	0.50	0.25
26. Primary bract color	3	8	0.25	0.87	0.22
27. Primary bract texture	2	8	0.25	0.87	0.22
21. Inflorescence type	4	12	0.25	0.83	0.21
52. Petal orientation at anthesis	3	7	0.29	0.72	0.21
58. Types of pollen grains	6	19	0.21	0.58	0.12
25. Primary bract margin	2	13	0.15	0.78	0.12
31. Floral bract color	4	20	0.20	0.56	0.11
36. Floral bract carinate	3	13	0.23	0.47	0.11
34. Terminal spine in the apex of the floral bract	3	17	0.18	0.59	0.10
30. Floral bract margin	2	9	0.22	0.46	0.10
14. Scape bract differentiation into sheaths and blades	2	4	0.25	0.40	0.10
41. Sepal color	5	26	0.15	0.56	0.09
55. Ovary color	4	15	0.20	0.43	0.09
7. Leaf margin	2	6	0.17	0.50	0.08
43. Terminal spine apex of the sepals	3	16	0.13	0.64	0.08
1. Mature leaf length	3	17	0.12	0.62	0.07
35. Floral bract shape (length/width ratio)	4	29	0.14	0.50	0.07
22. Flowers congested on rachis or inflorescence branches	2	11	0.09	0.75	0.07
32. Floral bract texture	2	15	0.13	0.50	0.07
37. Shape of floral bract relative to the flower	2	18	0.11	0.60	0.07
60. Rosette forming a water impounding tank	2	5	0.20	0.33	0.07
50. Petal appendage	4	25	0.12	0.53	0.06
47. Petal color	5	28	0.14	0.44	0.06
40. Flower indumentum	3	17	0.12	0.53	0.06
53. Ovary cross section	3	20	0.10	0.61	0.06
33. Floral bract apex (excluding terminal spine)	3	27	0.11	0.53	0.06
12. Scape	3	10	0.20	0.27	0.06
18. Scape bract apex (excluding the terminal spine)	3	8	0.13	0.42	0.05
48. Petal apex	3	22	0.09	0.57	0.05
20. Inflorescence rachis color	2	14	0.07	0.67	0.05
23. Flower arrangement along the rachis or inflorescence branches	2	10	0.10	0.47	0.05
51. Petal with lateral folds on the adaxial surface	2	13	0.08	0.59	0.05
3. Number of leaves per rosette	3	22	0.09	0.47	0.04
19. Inflorescence length excluding the naked scape (cm)	3	25	0.08	0.53	0.04
17. Scape bract texture	2	11	0.09	0.44	0.04
59. Habit	2	5	0.20	0.20	0.04
9. Leaf apex shape (excluding terminal spine)	4	19	0.16	0.24	0.04
15. Scape bract margin	2	15	0.07	0.58	0.04
13. Scape bracts	2	16	0.06	0.56	0.04
38. Flower length (without the pedicels)	3	28	0.07	0.49	0.04
45. Sepals carinate	2	12	0.08	0.39	0.03
4. Leaf ornamentation	2	9	0.11	0.27	0.03
57. Filament adnation to petals	3	28	0.07	0.40	0.03
16. Scape bract color	2	18	0.06	0.49	0.03
49. Petal shape	2	20	0.05	0.55	0.03
44. Sepal symmetry	2	19	0.05	0.47	0.03
8. Number of spines per 5 cm length of margin	3	27	0.07	0.29	0.02
42. Sepal apex	2	21	0.05	0.44	0.02
2. Blade and sheath	2	14	0.07	0.28	0.02
46. Sepal connation	2	13	0.08	0.25	0.02
5. Alteration in leaf color during anthesis	2	2	0.50	0	0
11. Phyllotaxy	2	1	1.00	0	0

is a xeromorphic character, and as such, possesses more ecological than taxonomic significance.

CLADE 2

This is a large and highly heterogeneous clade (Fig. 1) containing members of four *Aechmea* subgenera (*Aechmea, Lamprococcus, Ortgiesia, Platyaechmea*) and four additional genera (*Hohenbergia, Portea, Streptocalyx, Quesnelia*). The genera *Hohenbergia* and *Portea* as well as *Aechmea* subg. *Lamprococcus* and *Platyaechmea* are restricted to this clade. All other included genera and subgenera have representatives in other clades as well.

All investigated species of *Hohenbergia* (5 of 50 spp. sampled) are found in an unsupported group that also includes three species of *Aechmea* subg. *Aechmea*. *Aechmea marauensis* is placed as sister species of *H. disjuncta*, while two other species within subgenus *Aechmea* (*A. angustifolia* and *A. stelligera*) have a more basal position in this subclade. Traditionally, *Hohenbergia* is characterized by its inflorescence pattern with multiple branches, congested flowers, and floral bracts covering ovaries and sepals (Smith & Downs, 1979). Of these characters, the synapomorphies of twice (or more) branching inflorescences and congested flowers (characters 21 and 22, respectively) define the clade formed by *Hohenbergia* species plus *A. marauensis*. *Hohenbergia* has been treated as closely related to *Aechmea* subg. *Aechmea*, or placed as a separate subgenus or section of *Aechmea* (Baker, 1879, 1889). Our analysis has some agreement with the old classifications proposed by Baker (1879, 1889); however, additional sampling within *Hohenbergia* is needed.

The genus *Portea* (4 of 9 species sampled) also forms an unsupported clade nested within *Aechmea*, clade 2 (Fig. 1). *Portea*, like *Hohenbergia* subg. *Hohenbergia*, is restricted in distribution to the east coast of Brazil (northeast and southeast regions), and it shares many morphological characters with species of *Aechmea* subg. *Aechmea*. *Portea petropolitana* was treated within subgenus *Aechmea* by Baker (1889). Due to its multiporate pollen, Mez (1892, 1896, 1935) considered *Portea* to be closely related to *Gravisia*, a genus synonymized under *Aechmea* (Smith & Downs, 1979).

Two of three *Streptocalyx* species (3 of 14 total) in our analysis also occur in an unsupported clade nested within *Aechmea*. The third species (*S. floribundus*) is found in clade 9 (Fig. 1), the basalmost clade in the ingroup. *Streptocalyx* has been treated as a distinct genus (e.g., Smith & Downs, 1979) or submerged within *Aechmea* (Smith & Spencer, 1992). Our results suggest that *Streptocalyx* (sensu Smith & Downs, 1979) may not be monophyletic, and that this taxon has affinities with at least two distinctly different elements of *Aechmea*.

Only one species of *Lymania* (7 total) was included here. *Lymania* is generally accepted as monophyletic based on a sulcate ovary (Read, 1984), and a syndrome of floral and vegetative characters. Species of *Lymania* have either been recently described in the genus or transferred from either *Aechmea* subg. *Lamprococcus* or from the genus *Araeococcus* Brongn. The only exemplar included here is in the most strongly supported clade (94% bootstrap) within the ingroup, along with three species of subgenus *Lamprococcus*.

CLADE 3

This clade (Fig. 1) consists of *Quesnelia arvensis* and *Q. quesneliana* (subg. *Quesnelia*) on a well supported branch (bootstrap of 91%) with *Aechmea vanhoutteana* (subg. *Pothuava*) and *Q. edmundoi* var. *edumundoi* (subg. *Billbergiopsis*) as the sister group. The close affinity among *Q. arvensis, Q. quesneliana*, and *A. vanhoutteana* was already noted by Baker (1879, 1889), who treated *A. vanhoutteana* within *Quesnelia*. Wendt (1997) also stressed the close relationship among these species, based on the pattern of inflorescence and characters related to scape, floral bracts, petals, and petal appendages. Clade 3 is defined by a single homoplasious synapomorphy (character 16, pale or green scape bracts) and received no significant bootstrap support.

CLADE 4

Formed by three species of *Aechmea* subg. *Ortgiesia* (Fig. 1), this clade is supported by two homoplasious synapomorphies (characters 44, symmetric or slightly asymmetric sepals; 46, connate sepals above 1/3 of their length). Although connate sepals has been a diagnostic character for *Aechmea* subg. *Ortgiesia* by Mez (1892, 1896, 1935) and Smith and Downs (1979), the monophyly of the entire subgenus is not supported by our results. Two other *Ortgiesia* members (*A. burle-marxii, A. coelestis*) were placed distantly from each other as well as clade 4.

CLADE 5

This clade (Fig. 1) comprises species of *Aechmea* (subg. *Pothuava*), *Billbergia, Fernseea*, and *Quesnelia* (subg. *Billbergiopsis*). Clade 5 is defined by

two homoplasious synapomorphies (characters 38, flowers longer than 3.5 cm; 42, acute sepals). The genus *Billbergia* (6 of 62 sampled) appears monophyletic with a close relationship to *Fernseea*. The synapomorphies supporting *Billbergia* are all floral (characters 33, rounded floral bract apex; 35, broadly ovate floral bracts; 42, rounded sepal apex; 52, recurved petals in anthesis; 55, white or green ovaries; 56, filiform filaments), though only recurved petals have been previously used as a diagnostic character for the genus (Smith & Downs, 1979). The close relationship between *Billbergia* and *Fernseea* is supported by the presence of colpate pollen grains (character 58), among other synapomorphies (characters 16, rose or red scape bracts; 43, terminal spine of the sepals absent or much reduced; 44, sepals symmetric or slightly asymmetric; 47, red or rose petals; 48, rounded petal apex). This is in agreement with Mez (1892, 1896, 1935), who placed these two genera in subtribe Sulcatae due to this particular pollen morphology.

Species from *Aechmea* subg. *Pothuava* and *Quesnelia* subg. *Billbergiopis* comprise the remainder of clade 5. The polyphyletic status for both *Aechmea* subg. *Pothuava* and *Quesnelia* (Fig. 1) is reflected both by disjunct positions of member taxa on the consensus tree, and by the number of additional steps to make these taxa monophyletic (76 steps for *Pothuava*; 35 steps for *Quesnelia*). *Aechmea* subg. *Pothuava* has been variably treated at the generic, sectional, and subgeneric levels within *Aechmea* (see review in Wendt, 1997). Subgenus *Pothuava* consists of ca. 20 species occurring in two centers of geographic distribution: one in southern Brazil and the other in northwestern South America into Central America (Smith & Downs, 1979). Species distributed in these two centers possess very few morphological affinities but have been traditionally treated in the same subgenus (Wendt, 1997). The placement of subgenus *Pothuava* species on the consensus tree may correlate with the disjunct pattern of distribution observed for the subgenus. Those species of subgenus *Pothuava* in clade 5 (*A. allenii*, *A. drakeana*, *A. fraseri*, *A. involucrata*) are from western South America and Central America, whereas the Brazilian *Pothuava* species (*A. alopecurus*, *A. bocainensis*, *A. brueggeri*, *A. guaraparaiensis*, *A. ornata*, *A. pineliana*, *A. pectinata*, *A. vanhoutteana*) show unresolved relationship or lie in other clades.

Baker (1889) and Mez (1892, 1896) were the first authors to argue that *Quesnelia* constitutes a natural group. Mez (1892, 1896) stressed that *Quesnelia* subg. *Billbergiopsis* shows greater affinity to *Billbergia* than to *Quesnelia* subg. *Quesnelia*. Our results suggest that *Quesnelia* (sensu Smith & Downs, 1979) may not be monophyletic.

CLADE 6

The three sampled species of subgenus *Chevaliera* are placed in a moderately supported clade (bs. 76%; Fig. 1). *Chevaliera* sensu Smith and Downs (1979) is characterized by the lack of, or reduction in, petal appendages. From the synapomorphies that define clade 6 (characters 1, leaves greater than 100 cm; 7, leaf margin with spines greater than 3 mm; 34, terminal spines not exceeding floral bract length; 45, sepals with keels; 57, filaments adnate to the petals from their mid-point), none had previously been used as diagnostic. Relationship between *Chevaliera* and the other clades is unresolved in the consensus tree.

CLADE 7

Only 2 of 11 species of *Aechmea* subg. *Macrochordion* were sampled, but the results suggest that this subgenus may be monophyletic (Fig. 1). Synapomorphies that define the group include these characters (32, coriaceous floral bract; 40, dense indumentum covering floral parts; 43, unarmed sepals; 53, circular ovaries). Smith and Downs (1979) used unarmed sepals as diagnostic for subgenus *Macrochordion*. Wendt (1997) discussed a close relationship between *Aechmea* subg. *Macrochordion* and some Brazilian species of subgenus *Pothuava* (*A. alopecurus*, *A. brueggeri*, *A. guaraparaiensis*, *A. ornata*, *A. pineliana*) based on their simple strobilate inflorescences, but that putative relationship appears equivocal here.

CLADE 8

This clade consists of the two species sampled from the genus *Ronnbergia* (Fig. 1). Like *Streptocalyx*, *Ronnbergia* (sensu Smith & Downs, 1979) lacks petal appendages. Three synapomorphies define the clade (characters 6, petiolate leaf blades; 7, leaf margins with less than five spines; 10, channeled false midrib), though only the first character is without homoplasy. *Ronnbergia* is a small genus of 11 species characterized by a strong geographic disjunction. Eight species have distributions restricted to Central America and adjacent northwestern South America (Colombia to Ecuador), where they probably originated (Benzing, 2000). The remaining species (Pereira & Penna, 1985; Martinelli & Leme, 1987; Leme, 1999) are endemic to northeastern Brazil in Bahia State. The *Ronn-*

bergia clade received moderate support (bs. 69%); however, the three Brazilian species were not sampled in this study, implying monophyly for the non-Brazilian part of the genus. Benzing (2000) argued that this pattern of geographic disjunction exhibited by some Bromelioideae might suggest erroneous systematics rather than ancient or more recent long-distance dispersals. Conversely, Leme (1999) has suggested that the Atlantic Rain Forest flora of northeastern Brazil has been deeply influenced by the Amazonian flora, and thus the presence of *Ronnbergia* in Brazil is not unexpected. However, Leme (1999) did stress that new investigation must be done to elucidate the natural placement of these three Brazilian *Ronnbergia* species compared with *Aechmea*.

CLADE 9

Streptocalyx floribundus, *Aechmea lingulata* (subg. *Aechmea*), and *A. burle-marxii* (subg. *Ortgiesia*) form a clade that holds these taxa sister relative to the remaining ingroup (Fig. 1). The relationships between *A. lingulata* and *A. burle-marxii* received good support (bs. 85%); however, with *S. floribundus* the clade is unsupported and defined by the homoplasious synapomorphies: long inflorescences, greater than 30 cm (character 19) and lax disposition of the flowers on the inflorescence branches (character 22). These results agree with Smith and Spencer (1992), who reduced *Streptocalyx* (sensu Smith & Downs, 1979) under *Aechmea*, arguing that the occurrence of petal appendages by itself is not enough to delimit *Streptocalyx* as a distinct genus. The validity of the presence versus absence of petal appendages as the sole character for generic delimitation was first questioned by Brown and Terry (1992). According to them, petal appendages are the last structures formed in the flower, representing terminal ontogenetic characters. This kind of character may be more susceptible to evolutionary change because a modification or reversal in such a terminal character will not affect preceding developmental steps (Sachs, 1982). For bromeliads, Brown and Terry (1992) argued that petal appendages can be lost and/or gained repeatedly without affecting the development and function of other floral organs and that homoplasy may be realized more easily and without impact on the ontogeny of earlier formed, nonterminal characters.

TAXONOMIC IMPLICATION

The results, while somewhat provisional, offer the first explicit demonstration, with few exceptions (i.e., *Aechmea* subg. *Chevaliera* and *Macrochordion*), that the subgenera of *Aechmea* do not otherwise correspond to monophyletic groups (Fig. 1). Therefore, the proposals of Smith and Kress (1989, 1990) to elevate all *Aechmea* subgenera (sensu Smith & Downs, 1979) to generic rank are not supported. The morphological characters traditionally employed in generic and infrageneric delimitations within Bromelioideae display high levels of homoplasy (see Table 3). This degree of character homoplasy, in concert with the various emphases placed on different characters, is likely to be the reason for the divergent previous classifications proposed within Bromelioideae. Presumably the radiation of Bromelioideae into many diverse, even physically extreme environments, invoked a multitude of abiotic and biotic pressures that resulted in certain attributes arising independently several times (Terry et al., 1997). Many aspects of vegetative structure and function are homoplasious, as are most of the many pollination syndromes recorded for the family (Benzing, 2000).

The phylogenetic hypothesis presented here indicates that traditional generic and subgeneric delimitations in Bromelioideae need serious reconsideration. However, as indicated earlier, these results best represent a first approximation, provisional in nature, and do not merit any reorganization or nomenclatural action. We are actively expanding both the taxon and character samples presented here, and augmenting these with DNA sequence data to develop a more robust phylogenetic analysis of *Aechmea* and related genera within Bromelioideae.

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APPENDIX 1. Morphological characters and states used in the cladistic analysis.

1. Mature leaf length: 0 = short leaves, to 50 cm; 1 = leaves over 50 to 100 cm; 2 = very long leaves, over 100 cm. Bromeliads typically consist of a short stem bearing alternate, closely placed, leaves. The length of mature leaves provides an accurate indication of rosette size.
2. Blade and sheath: 0 = not differentiated or only slightly so; 1 = differentiated.
3. Number of leaves per rosette: 0 = more than 15; 1 = 8 to 15; 2 = less than 8. The number of leaves can vary greatly within the genera analyzed and is not related to the size of the plants (i.e., not all smaller plants produce fewer leaves, and vice versa). This character needs to be scored from living plants, before the vouchers are prepared.

4. Leaf ornamentation: 0 = absent, leaf blades uniformly green; 1 = present. Leaf color is exceptionally variable and vivid among bromeliads, and often involves trichomes. Several species are distinguished by irregular blotching or cross-banding patterns.
5. Alteration in leaf color during anthesis: 0 = yes; 1 = no. Independent of leaf ornamentation, some taxa display a change in leaf color during anthesis presumably to help in pollinator attraction. Frequently, the color change increases toward the center of the rosette, e.g., *Aechmea recurvata*; sometimes the color change involves the distal end of leaf blades, e.g., *A. pectinata*.
6. Leaf form: 0 = linear; 1 = petiolate; 2 = filiform. Most Bromelioideae have linear leaves. Petiolate blades (blade strongly narrowed at base), similar to that of some dicots, and filiform leaves (with narrow, involute blades) are found in such genera as *Ronnbergia* and *Acanthostachys*, respectively.
7. Leaf margin: 0 = spines more than 3 mm long; 1 = to 3 mm.
8. Number of spines per 5 cm length of margin (at the leaf middle point): 0 = 5 spines or less; 1 = 6 to 9; 2 = 10 or more. Leaves with armed margins characterize most Bromelioideae, and the length and density of these spines are variable within and between genera.
9. Leaf apex shape (excluding terminal spine): 0 = acute; 1 = rounded; 2 = retuse; 3 = long-attenuate. The leaf apex for *Aechmea* and related genera shows great variation with the more common types being acute and rounded. During plant development we observed that leaf apex shape could change. Young plants may have an acute apex in the first-formed leaves, while latter ones will have a rounded apex, e.g., *Aechmea nudicaulis*. Here only mature leaves collected from the middle part of the rosette were scored.
10. A false midrib: 0 = absent; 1 = slightly to strongly channeled. Leaves may possess a mid-longitudinal region thickened by a succulent, multiply layered hypodermis. A channeled false midrib is commonly associated with the genus *Ronnbergia*, as petiolate blades.
11. Phyllotaxy: 0 = spiral; 1 = distichous.
12. Scape: 0 = erect and exceeding the rosette; 1 = prostrate or slightly curved; 2 = erect and short (hidden in the center of the rosette). Erect scapes are more common in those genera analyzed except for *Billbergia*, where prostrate scapes are present in most species. Very short scapes sunken in the center of the rosette characterize the outgroup *Cryptanthus*, but may also be found in some *Acanthostachys*, *Aechmea*, *Ronnbergia*, and *Streptocalyx*.
13. Scape bracts: 0 = imbricate, exceeding the internode above and covering the scape; 1 = not imbricate, shorter than internode above, leaving the scape exposed.
14. Scape bract differentiation into sheaths and blades: 0 = differentiated; 1 = not differentiated. Some scape bracts resemble leaves, and a distinct sheath and blade can be recognized.
15. Scape bract margin: 0 = entire; 1 = armed.
16. Scape bract color: 0 = green or pale green; 1 = rose or red. Frequently bromeliads show colorful scape bracts, which can help in pollinator attraction and even seed dispersal when they remain brightly colored after the flowering period.
17. Scape bract texture: 0 = coriaceous; 1 = membranaceous or chartaceous. Usually the bromeliad leaves are coriaceous and some scape bracts show similar texture, while others are thinner.
18. Scape bract apex (excluding the terminal spine): 0 = acute; 1 = rounded; 2 = long attenuate.
19. Inflorescence length, excluding the naked scape (cm): 0 = to 10; 1 = over 10 to 30; 2 = over 30. Except for the outgroup species, where inflorescences never exceed a few centimeters, this character varies greatly within and among the genera analyzed. For individuals that show great variation in this character (e.g., *Aechmea multiflora* and *A. sphaerocephala* have inflorescences that elongate as anthesis proceeds), an average was taken of at least two specimens observed in different flowering stages.
20. Inflorescence rachis color: 0 = white, green, or rachis color not visible (covered by congested flowers); 1 = rose or red.
21. Inflorescence type: 0 = simple (racemes or spikes); 1 = once branched; 2 = two or more times branched; 3 = corymbose shape (simple or branched).
22. Flowers congested on rachis or inflorescence branches: 0 = no; 1 = yes.
23. Flower arrangement along the rachis or inflorescence branches: 0 = polystichous; 1 = distichous.
24. Primary bract: 0 = absent; 1 = present. Branched inflorescences have one bract at the base of each branch. The primary bract is the one present in the lowest or first branching. Simple inflorescences do not have a primary bract.
25. Primary bract margin: 0 = armed; 1 = entire. If primary bracts are absent, characters 25–28 were coded as inapplicable.
26. Primary bract color: 0 = greenish or pale; 1 = yellow or orange; 2 = rose or red.
27. Primary bract texture: 0 = coriaceous; 1 = membranaceous or chartaceous.
28. Primary bract apex: 0 = acute; 1 = long attenuate; 2 = rounded.
29. Floral bracts: 0 = present; 1 = absent. Floral bracts are characteristic for most Bromelioideae and they can vary from much reduced (e.g., *Aechmea* subg. *Lamprococcus*) to well developed, sometimes exceeding the flowers (e.g., *Aechmea* subg. *Chevaliera*).
30. Floral bract margin: 0 = entire; 1 = armed. If floral bracts are absent, characters 30–37 were coded as inapplicable.
31. Floral bract color: 0 = green, pale green, or castaneous; 1 = yellow or orange; 2 = rose or red; 3 = blue, lilac, or purple.
32. Floral bract texture: 0 = membranaceous or chartaceous; 1 = coriaceous or fleshy.
33. Floral bract apex (excluding terminal spine): 0 = rounded; 1 = long-attenuate; 2 = acute.
34. Terminal spine in the apex of the floral bract: 0 = absent or much reduced; 1 = present, but shorter than the bract; 2 = equaling or longer than the bract. The majority of species analyzed have floral bracts with terminal spines. These spines can be very short (*Billbergia*) or well developed, sometimes being longer than the bract.
35. Floral bract shape (length/width ratio): 0 = broadly ovate (1:1); 1 = very broadly ovate (1:2); 2 = narrowly ovate (3:1); 3 = ovate (2:1).

36. Floral bract carinate: 0 = no; 1 = yes, 1 keel; 2 = yes, 2 or 3 keels.
37. Shape of floral bract relative to the flower: 0 = flat; 1 = concave (enfolding ovaries, sepals, and sometimes the whole flower). Concave floral bracts may occur in many Bromelioideae taxa and are frequently related to the bract shapes as broadly ovate (1:1) and very broadly ovate (1:2). Bracts enfolding only the ovary or most of the calyx are the most common condition (e.g., *Aechmea bromeliifolia*).
38. Flower length (without the pedicels): 0 = less than 2 cm; 1 = 2 to 3.5 cm; 2 = over 3.5 cm.
39. Pedicel: 0 = absent; 1 = present. In *Aechmea*, pedicellate flowers are found in subgenus *Podaechmea* and some species of *Lamprococcus*. For other genera pedicellate flowers characterize *Portea* and *Fernseea*. Flowers without a pedicel are more common within the subfamily.
40. Flower indumentum: 0 = absent; 1 = sparse with surfaces remaining visible; 2 = dense (pilose or lanuginose) completely concealing the epidermal surfaces. Most species analyzed present sparse indumentum covering floral structures. Dense indumentum characterizes *Aechmea* subg. *Macrochordion*, some species of subgenus *Pothuava*, and genus *Hohenbergia*. These species show lanuginose inflorescences, and this characteristic is maintained both in cultivation and the field.
41. Sepal color: 0 = white, green, or pale green; 1 = blue, lilac, or purple; 2 = red or rose; 3 = yellow or orange; 4 = bicolored, frequently green-toned with a contrasting colored tip.
42. Sepal apex: 0 = rounded; 1 = acute.
43. Terminal spine, apex of the sepals: 0 = absent or much reduced; 1 = present, but shorter than the sepal; 2 = equaling or exceeding the sepal. Sepals without apical spines occur in a few Bromelioideae (*Quesnelia*, *Aechmea* subgenera *Macrochordion*, *Lamprococcus*). Apical spines can be very short to well developed, sometimes longer than the sepal length. This last characteristic (2) is present in most of *Aechmea* subg. *Ortgiesia* and in some species of subgenus *Pothuava*.
44. Sepal symmetry: 0 = symmetric or slightly asymmetric; 1 = strongly asymmetric. Most *Aechmea* and related genera possess a lateral wing on sepals making them strongly asymmetric.
45. Sepals carinate: 0 = yes; 1 = no.
46. Sepal connation: 0 = free; 1 = connate by 1/3 or more of its length.
47. Petal color: 0 = white, cream, or pale green; 1 = blue, lilac, or purple; 2 = red or rose; 3 = yellow or orange; 4 = bicolored: mostly white, yellow, or green, and the apex blue.
48. Petal apex: 0 = rounded; 1 = acute; 2 = retuse.
49. Petal shape: 0 = linear; 1 = spatulate.
50. Petal appendage: 0 = absent; 1 = pouch- or sac-like; 2 = fringed; 3 = tongue-like. Some flowers possess tissue outgrowths on the adaxial surface of petals called petal appendages. Petal appendages are absent in *Streptocalyx*, *Fernseea*, *Ronnbergia*, and *Cryptanthus* (outgroup).
51. Petal with lateral folds on the adaxial surface: 0 = absent; 1 = present. Some petals present longitudinal callus-like outgrowths called lateral folds that can occur independently of the presence of petal appendages, i.e., *Aechmea* subg. *Chevaliera*, or in combination with them, i.e., *Billbergia*. Except for *Hohenbergia*, in most species analyzed the presence of lateral folds was related to the presence of petal appendages. The outgroup genus does not possess petal appendages or lateral folds.
52. Petal orientation at anthesis: 0 = erect or cucullate; 1 = spreading; 2 = recurved. Erect petals are observed for most species sampled and are constant for *Aechmea* subgenera *Macrochordion* and *Chevaliera*. Spreading petals are present in some species of *Quesnelia*, *Lymania*, *Acanthostachys*, *Streptocalyx*, and *Ronnbergia*, being constant for *Cryptanthus* (outgroup). Recurved petals are a remarkable characteristic for *Billbergia*.
53. Ovary cross section: 0 = terete; 1 = trigonous; 2 = laterally compressed.
54. Ovary surface: 0 = smooth; 1 = finely verrucose; 2 = longitudinal furrows.
55. Ovary color: 0 = white or green; 1 = yellow or orange; 2 = rose or red; 3 = blue, lilac, or purple.
56. Filament shape: 0 = complanate; 1 = filiform.
57. Filament adnation to petals: 0 = adnate by mid-filament; 1 = adnate above mid-filament; 2 = almost free (adnate for less than half of the filament).
58. Types of pollen grains: 0 = inaperturate; 1 = sulcate; 2 = 2 pores; 3 = 3 pores; 4 = 4 pores; 5 = 5 or more pores. Some species are polymorphic for this character with more than one type in the same anther (see Appendix 2). This occurred in different genera (e.g., *Acanthostachys*, *Streptocalyx*, *Hohenbergia*, and in *Aechmea* subg. *Platyaechmea*). For the outgroup (*Cryptanthus*), inaperturate grains are characteristic.
59. Habit: 0 = obligate terrestrial or saxicolous; 1 = facultative epiphytes.
60. Rosette forming a water impounding tank: 0 = no; 1 = yes.

Appendix 2. Matrix of morphological data. Character numbers refer to those in Appendix 1. Character state unknown is indicated with a question mark, and inapplicable with a dash. Polymorphic taxa are coded with the following symbols: A = (0 & 2), B = (2 & 3), C = (2 & 4), D = (3 & 4), E = (4 & 5).

	Character number					
	1	1111111112	2222222223	3333333334	4444444445	5555555556
Taxa	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Acanthostachys pitcairnioides	1110121130	0211101000	3100----01	0101201201	0110004100	1120000210
Acanthostachys strobilacea	1120121130	0110000100	0100----01	2121301101	3110003011	0020000B10
Aechmea allenii	1010101200	0011111000	0100----00	2021200201	2111101112	?0100??111
Aechmea alopecurus	1010101200	0001010010	0100----00	0002111002	2111101212	1020001111
Aechmea angustifolia	1110100000	0001111011	1011111000	0021101001	0010103113	0010002411
Aechmea aquilega	1100101200	0001100021	2101110000	1121311200	3111003103	1010000511
Aechmea blanchetiana	2110101200	0001100021	2011110000	2121211200	3111103103	0010000501
Aechmea bocainensis	1100101200	0001111000	0100----00	2011011001	2011001103	0010000B11
Aechmea bromeliifolia	1100101200	0001111000	0100----00	0100121102	3001103012	1000000B11
Aechmea brueggeri	1100101200	0001011000	0100----00	0101021001	0110101112	1020000201
Aechmea burle-marxii	0110101110	0011001110	1001001100	0010200001	0111110110	1100000211
Aechmea caesia	0110100000	0001011101	1101011101	2010301001	2001101202	?000000211
Aechmea calyculata	0110101100	0011111000	0100----00	2020300001	3020113211	1000101211
Aechmea chantinii	0101100110	0001011011	1111011000	2100011101	3000103112	1010200A11
Aechmea coelestis	0110101210	0011111101	1001111100	2020300001	2020111211	1010202211
Aechmea correia-araujoi	0101101110	0111111010	2011111000	0000001100	0001103213	0000000?11
Aechmea dealbata	0011101200	0011011100	1101011101	2010201101	2000101212	1010001211
Aechmea distichantha	1100101200	0001101011	1111111000	2001101001	2111111213	0000001B11
Aechmea drakeana	1110101200	0001101001	0000----00	2010200201	2111101101	1101202211
Aechmea eurycorymbus	2100101200	0001100021	2001100000	2021200200	3111103103	1010000511
Aechmea fasciata	0011101110	0011011100	1101011101	2010201101	2000111212	1010000211
Aechmea fosteriana	0111101210	0011111011	1001111000	2100001100	0011103203	0010000211
Aechmea fraseri	1010101200	0011001001	0000----00	2011200201	2011101101	0100201111
Aechmea fulgens	0110101210	0011111011	101111101-	-------100	2001101213	0001201D11
Aechmea gamosepala	0100101000	0011101111	0000----00	2020200001	2020111211	1000201211
Aechmea guarapariensis	1100101210	0001011010	0100----00	0002121001	3110100103	0020001211
Aechmea gurkeniana	1110101200	0001011011	1001011000	2100001100	2001103203	0000200211
Aechmea involucrata	1010101200	0011011011	0000----01	2011200101	2111111102	1100201111
Aechmea lingulata	1000101200	0011001120	1001101100	0010200001	0121100110	1100000211
Aechmea marauensis	1110101200	0001110011	2111110000	3101011100	1011001013	1010000511
Aechmea mariae-reginae	1100101200	0001011010	0100----00	0010200101	0011101211	102?001?11
Aechmea miniata	0110101200	0011111001	101111101-	-------001	2000111213	0000201211

Appendix 2. Continued.

Taxa	Character number					
	1	1111111112	2222222223	3333333334	4444444445	5555555556
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Aechmea multiflora	2000100000	0000000020	0100----01	2101220201	0011000103	1020002111
Aechmea mutica	1100101200	0001110010	1101111000	2021001102	0000101203	0000001501
Aechmea nudicaulis	1010101120	0001011001	0000----00	2010000001	3011103012	1010102211
Aechmea orlandiana	0101100100	0011011000	1101011000	2120001100	2111103201	0010000211
Aechmea ornata	1100101200	0000010010	0100----00	0102021101	0010111002	0000001?11
Aechmea pectinata	1010001100	0001000000	0100----01	0110200101	0100000113	1020002C11
Aechmea penduliflora	0110101200	0011011011	1011011000	0000000001	0101103112	1000100011
Aechmea pineliana	1100101200	0001011000	0100----00	0002011001	0010103112	1000000211
Aechmea purpureorosea	1111101100	0011101010	1011111000	2021300101	2010101001	1010201211
Aechmea ramosa var. *festiva*	2100101200	0011111011	2011111000	2001000000	3111103111	1000200D11
Aechmea ramosa var. *ramosa*	2100101200	0001110021	2011110000	0001000100	0011103113	1000000E11
Aechmea recurvata	0100011130	0211101000	3100----01	2020200100	2010111202	1010001210
Aechmea rubens	2110101200	0001100021	2101110000	2121311200	3111003103	1010000511
Aechmea saxicola	2100100000	0000000010	0100----01	2111220201	0111000110	1020000111
Aechmea sphaerocephala	2100100100	0000010010	0100----00	0121021201	0111001103	1000000111
Aechmea stelligera	1100101100	0001111021	2001111000	2001000101	3011103101	1010001511
Aechmea triangularis	1100101130	0011011000	0100----00	0100021002	0000111212	1000001211
Aechmea vanhoutteana	1100100100	0001100010	0100----00	2010001002	2100101213	0010001411
Aechmea warasii	1110101210	0111101011	101111101-	-------100	2001101003	0001201D11
Aechmea weilbachii var. *albipetala*	1110101000	0001111011	1011111000	2000001100	2011100110	1000300411
Aechmea weilbachii var. *weilbachii*	1100101000	0001111011	1011111000	2000001000	0001111213	0000202211
Aechmea werdermannii	1100101000	0001110021	2001110000	2021000100	3011103103	1000001511
Billbergia amoena	0110101010	0001111010	1001111000	0000200201	4000104003	1212012111
Billbergia distachia	0010101000	0101111000	1001111000	0020000201	4000103003	1212012111
Billbergia elegans	0110101210	0101111001	1001010000	2000000201	4000103001	1212012111
Billbergia euphemiae	1010101100	0111111001	0000----00	2020000201	2000104001	1202012111
Billbergia pyramidalis	1110101100	0001111000	3100----00	0020000201	2000102001	1212012111
Billbergia sanderiana	0011101220	0101111011	1001111000	2020000201	4100104003	1212012111
Cryptanthus bromelioides	0010101230	0201?01?00	3100000100	0020200100	0100010000	0110012000
Cryptanthus pickelii	0110101230	0201?01?00	3100000100	0020311100	0100010010	0110011000
Fernseea itatiaiae	0110101231	0000011101	0000----00	2010200011	2100102000	0012202110
Hohenbergia catingae	1110101100	0011101011	2101111000	0021001001	0101101113	0010001211
Hohenbergia correia-araujoi	2111101100	0011111021	2101111000	0001001002	0011003003	0010000E11
Hohenbergia disjuncta	1110101200	0011010020	2101010000	0101011101	3011003213	0010000211
Hohenbergia ramageana	1100101100	0001111021	21011?1000	0101001001	0111101113	0010000211

Appendix 2. Continued.

Taxa	Character number					
	1	1111111112	2222222223	3333333334	4444444445	5555555556
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Hohenbergia stellata	1110101100	0001101010	2101101000	2121001101	2111001113	0010000411
Lymania azurea	0120101200	0011101001	101110101-	-------000	0001104010	1102000411
Portea alatisepala	1110101200	0001011011	2001011000	2010200210	1011111003	1000202511
Portea fosteriana	1110101200	0000011010	2001111000	2010200210	2011111003	1000200511
Portea leptantha	2100100000	0001100021	2001111000	0010200110	3111103103	1000000511
Portea petropolitana	2100101100	0001001011	2001111000	2010200210	1011101103	1000001511
Quesnelia arvensis	1100101200	0001001000	0100----00	2020201201	2001104213	0010000211
Quesnelia augusto-coburgii	1010101200	0111101120	0000----00	0010201200	2111101102	1112202211
Quesnelia blanda	1110101200	0011111000	0100----00	2020301201	2100101102	1010001211
Quesnelia edmundoi var. *edmundoi*	0100100200	0001101010	0100----00	1120301100	3000000203	0020000211
Quesnelia edmundoi var. *rubrobracteata*	1100100110	0001111010	1101110000	2100001100	3000001201	0010000211
Quesnelia lateralis	1010101210	0011111100	0100----00	2020301201	2000101102	1010001211
Quesnelia liboniana	0020101200	0011101101	1000----00	2010200201	2001001102	1000200211
Quesnelia marmorata	1021101210	1111111011	1001111000	0020000101	1000101211	1000000211
Quesnelia quesneliana	1100101200	0001001010	0100----00	2020201201	2001104213	0010000211
Quesnelia seideliana	1010101200	0011111100	0100----00	0020301201	0100101102	1010000211
Ronnbergia deleonii	1110111001	0001001000	3100----00	0010200101	0111100010	1100001201
Ronnbergia morreniana	0111111001	00011?1000	0100----00	0020200101	0101111110	1100001211
Streptocalyx floribundus	2101101200	0001000020	2001000000	0101101100	0111100110	1100001D11
Streptocalyx longifolius	1110101230	0011101010	1111011001	2021201101	2111000100	1010200010
Streptocalyx poeppigii	1100101200	0001011011	1011011000	2020100201	2011101100	1000200B11

WHAT IS THE TAXONOMIC STATUS OF *POLYGONELLA*? EVIDENCE OF FLORAL MORPHOLOGY[1]

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ABSTRACT

A comparative morphological study of floral characters of the North American genus *Polygonella* and the four currently accepted sections of *Polygonum* s. str. (sect. *Polygonum*, sect. *Duravia*, sect. *Pseudomollia*, sect. *Tephis*) has been carried out with light microscopy (LM) and scanning electron microscopy (SEM). Flowers were investigated for macromorphological characters, tepal epidermal characters, pollen, and fruit morphology and anatomy. Results demonstrate that the limits between both genera become blurred through section *Duravia* of *Polygonum*, especially in characters of pollen and fruit morphology. *Polygonum* sect. *Duravia* and *Polygonella* share a wealth of intergrading floral and vegetative characters at the macroscopic, as well as ultrastructural, level (pollen morphology, fruit morphology, flower structure, vegetative anatomy). These characteristics, especially the pollen morphology, are sharply delimited from section *Polygonum*. Evidence presented here allows for a broader concept of *Polygonum* s. str. to be adopted, with an extended section *Duravia* including subsections *Duravia* and *Polygonella*. A cladistic analysis of morphological characters supports two distinct clades, section *Polygonum* with subsections *Polygonum* and *Tephis*, and section *Duravia* with subsections *Duravia* and *Polygonella*.

Key words: cladistic analysis, *Duravia*, floral morphology, fruit, pollen, Polygonaceae, *Polygonella*, *Polygonum*, sectional classification.

The genus *Polygonella* Michx. contains about 9 to 11 species native to eastern North America, with a few western outliers. The genus was originally erected by Michaux in 1803 to accommodate a single species, *P. parvifolia* Michx. Since that date a number of North American genera were described independently for the Polygonaceae. Fischer and Meyer (1840: 144) described the genus *Gonopyrum* Fisch. & Mey. ex C. A. Mey. with one species (*G. americanum*). Rafinesque described several new genera in the Polygonaceae, which were eventually transferred into *Polygonella*, such as *Lyonia* Rafin. (1808: 352), *Phyllepidum* Rafin. (1808: 356), *Lyonella* Rafin. (1818: 266), *Phylepidum* Rafin. (1836: 51), and *Stopinaca* Rafin. (1837: 11). Gray (1845: 232) recognized the genus *Thysanella* with one species (*T. fimbriata*) originally placed in *Polygonum*. Nieuwland (1914: 171) created the genus *Psammogonum* for two species, *P. articulatum* Nieuwl. and *P. americanum* Nieuwl. Small (1896, 1909, 1913, 1924) described five new species in *Polygonella* and erected two additional genera (*Delopyrum* and *Dentoceras*). In 1933 he recognized 13 species under four distinct genera (*Polygonella*, *Delopyrum*, *Dentoceras*, and *Thysanella* A. Gray), while absorbing the other previously described genera. However, all were included by Horton (1963) under *Polygonella*, because he considered the differences used by Small (1896, 1909, 1924) to segregate these smaller genera not distinctive enough. The arguments used by Horton (1963) to recognize a single genus were mainly the homogeneity in anatomy and flower form against the heterogeneity in the neighboring genus *Polygonum*, although his views of the latter genus were doubtless much broader than in the present paper. An additional

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argument already used by Small (1897) is the fact that branching in *Polygonella* is internodal by adnation of the secondary axis to the main axis above a node, contrary to other members of the Polygonaceae. Eleven species are currently recognized. For population size and distribution we refer to Lewis and Crawford (1995). Horton (1963) did not consider the generic limits of *Polygonella*, nor did he make comparisons with taxa outside the genus. Meisner (1857) related *Polygonella* with *Atraphaxis* L. in a separate subtribe. Only later did authors consider it as related to *Polygonum* sensu lato (Bentham & Hooker, 1883; Dammer, 1893), although always as a distinct genus.

The most important distinctive characters of *Polygonella* enumerated in the literature are that the branches appear internodal by the fusion of their basal part to the main stem, the abruptly dilated inner filaments, the presence of solitary flowers on elongated pedicels at the nodes, the colored marcescent tepals, and conspicuous scarious bracts (Watson, 1873; Small, 1897; Rydberg, 1932; Graham & Wood, 1965; see Table 2). Horton (1963) added a few anatomical features, such as the very short vessel elements and a strongly reduced vascularization of the flower (as was observed by Vautier, 1949).

Horton recognized two subgenera in *Polygonella*, viz. subgenus *Polygonella* comprising the great majority of the species, and subgenus *Thysanella* with only one species (*Polygonella fimbriata* (Ell.) Horton) consisting of two varieties. Subgenus *Polygonella* was described as having two outer and three inner morphologically distinct tepals, pedicels without bracteoles within the ocreolae, and filaments that are dilated at the base, forming two lateral teeth. Subgenus *Thysanella* has two outer, one transitional, and two inner tepals, pedicels subtended by bracteoles within the ocreolae, and the filaments all alike and without teeth. Nesom and Bates (1984) considered the two varieties of *Polygonella fimbriata* as two valid species, *P. fimbriata* and *Polygonella robusta*. In a cladistic analysis, Lewis (1991, cited in Lewis & Crawford, 1995) found that *P. fimbriata* and *P. robusta* appear as a basal clade within *Polygonella*.

The circumscription of the genus *Polygonum* L. has changed considerably since its much broader circumscription by earlier authors. In recent approaches to the family Polygonaceae, the genus is currently segregated in the genera *Polygonum* s. str., *Fallopia* Adans., *Persicaria* Mill., with segregates *Aconogonon* (Meisn.) Rchb. and *Bistorta* Mill., and *Koenigia* L. (e.g., Haraldson, 1978; Ronse De Craene & Akeroyd, 1988; Brandbyge, 1993). Four sections are currently accepted within *Polygonum* s. str. (e.g., Dammer, 1893; Hedberg, 1946; Haraldson, 1978), viz. sections *Pseudomollia*, *Tephis*, *Polygonum* (= *Avicularia*), and *Duravia* (see Table 1). Ronse De Craene and Akeroyd (1988) recognized two sections only (*Polygonum*, *Tephis*), as they believed the distinctive characters to be unimportant in comparison to the inherent variability of section *Polygonum*. Haraldson (1978: 79) summarized the differences between the tribes of *Polygonum* s. str. in a table. She reported the presence of three staminodes besides five fertile stamens as a distinctive character for sections *Pseudomollia* and *Duravia*. Watson (1873) and Haraldson (1978) pointed out that section *Tephis* is more similar to section *Duravia* than to section *Polygonum*.

Section *Duravia* was erected by Watson (1873) for a single species, *Polygonum californicum*, on the basis of its supposedly distinctive achene structure (with a membranaceous pericarp). Small (1895) included four other species in his subgenus *Duravia* (*Polygonum bolanderi*, *P. greenei*, *P. parryi*, *P. bidwelliae*) on the basis of lacerate ochreae and spicate inflorescences. Greene (1904) elevated *Duravia* to generic rank on the basis of three distinctive characters (viz. solitary flowers, persistent styles, and absence of articulation at the base of the leaf blade). He accepted three other species (*D. bidwelliae*, *D. greenei*, and *D. bolanderi*) besides *D. californica*.

The taxonomy of North American *Polygonum*, sections *Polygonum* and *Duravia* alike, remains confused, as different populations tend to show wide gene flow and a high level of interbreeding (e.g., Mertens & Raven, 1965; Wheeler, 1938). Hickman (1984) tried to solve this problem by accepting two polymorphic species, *Polygonum polygaloides* and *Polygonum douglasii*, each with a number of subspecies that had been previously described under various species. He elevated section *Duravia* to the rank of subgenus with two sections, section *Duravia* with five species and section *Monticola* with the two heterogeneous species.

Hedberg (1946) described a distinct pollen type, the *Duravia*-type, for 18 species of *Polygonum* sensu lato, deviating from the other species of the genus, and including members of *Polygonella*. However, several species possessing the *Duravia*-type of pollen were placed by Small (1895) in his subgenus *Avicularia* (equivalent to sect. *Polygonum*). Based on the study of a limited number of species, Haraldson (1978) recognized section *Duravia* as distinct from section *Polygonum* by its petiole anat-

Table 1. Summary of the most important delimitations of *Polygonum* s. str. and *Polygonella* (full line indicates that certain sections were not considered by the authors).

Meisner (1857)	Bentham & Hooker (1883), Dammer (1893)	Small (1895, 1933)	Gross (1913)	Jaretzky (1925)
Sect. *Avicularia*	Sect. *Avicularia*	Subg. *Polygonum*	Sect. *Avicularia*	*Avicularia* sect. *Avicularia*
Sect. *Avicularia*	Sect. *Pseudomollia*	—	Sect. *Avicularia*	*Avicularia* sect. *Avicularia*
Sect. *Avicularia*	Sect. *Avicularia*	Subg. *Duravia*	Sect. *Avicularia*	*Avicularia* sect. *Avicularia*
Sect. *Tephis*	Sect. *Tephis*	—	Sect. *Tephis*	*Avicularia* sect. *Tephis*
Polygonella	*Polygonella*	*Polygonella, Dentoceras, Delopyrum*	*Polygonella*	*Polygonella*
—	—	*Thysanella*	—	—

omy and found it anatomically closer to *Polygonella* than to section *Polygonum*.

Other authors did not recognize the identity of section *Duravia*, mainly because of the observed existence of transitional forms between section *Duravia* and section *Polygonum* (see Dammer, 1893; Gross, 1913; Jaretzky, 1925; Graham & Wood, 1965; Ronse De Craene & Akeroyd, 1988; Table 1). Several North American species were retained in section *Polygonum* (Watson, 1873; Small, 1895), or no difference was made at the sectional level (Rydberg, 1932, 1954; Small, 1903, 1933; Kaul, 1986). Indeed, the taxonomy of section *Duravia* appears confusing and it is difficult to draw a sharp line between section *Polygonum* and section *Duravia*, especially in the annual species of section *Polygonum*. *Polygonella*, on the contrary, has been maintained as a distinct genus by all authors despite the fact that several distinctive features of *Polygonella* are found in *Polygonum* s. str., especially in the species that have been grouped under section *Duravia*. These characters include:

- The presence of a single unbranched vein in each tepal (Vautier, 1949; Horton, 1963; Graham & Wood, 1965; Ronse De Craene & Akeroyd, 1988);
- The corresponding vegetative anatomy of section *Duravia* and *Polygonella* (Haraldson, 1978);
- The lateral expansion of the (inner) filament bases does not occur in all species of *Polygonella*. In *Polygonella fimbriata* filaments are basally inflated as in *Polygonum* sect. *Polygonum* and section *Duravia*; the inner filaments of *Polygonella macrophylla* are intermediate (Horton, 1963);
- The similar epidermal cell morphology of the tepals (Ronse De Craene & Akeroyd, 1988; Hong et al., 1998);
- The pollen morphology of *Polygonella* and *Polygonum* sect. *Duravia* appears to be similar (Hedberg, 1946; Nowicke & Skvarla, 1977; Hong & Oh, unpublished). Hedberg (1946) found four species of *Polygonella* matching the pollen grains of *Polygonum* sect. *Duravia* ("*Duravia*-type"). However, he found one species, *Polygonella parvifolia* (= *Polygonella polygama*), that had pollen grains almost identical to section *Polygonum* ("*Avicularia*-type"), but he was not convinced of a close relationship, as important differences exist in habit and phytogeographical distribution. He concluded that there had been parallel development of the same pollen type in the two groups.
- The apparent trend for the outer stamens to become reduced or lost (a reduction of the total from eight to three; see also Ronse De Craene & Akeroyd, 1988); this trend is correlated with an expansion of the inner filament bases and occurs occasionally in *Polygonella* (Horton, 1963), *Polygonum* sect. *Duravia* (Wheeler, 1938), and section *Polygonum* (Trail, 1896; Ronse De Craene & Akeroyd, 1988). Gross (1913) mentioned one case of *Polygonella parvifolia* (= *Polygonella polygama*) with five stamens: three inner, and two outer (replacing the two pairs). An identical disposition is occasionally found in *Polygonum* sect. *Polygonum* (Vautier, 1949).

Ronse De Craene and Akeroyd (1988) briefly discussed the possibility of combining *Polygonella* and *Polygonum* s. str. into a single genus. In this paper we provide arguments for solving the problem, as more evidence has been gathered from dif-

Table 1. Extended.

Hedberg (1946)	Graham & Wood (1965)	Haraldson (1978)	Ronse De Craene & Akeroyd (1988)	Ronse De Craene & Hong (as proposed herein)
Sect. *Polygonum*	*Sect. Polygonum*	Sect. *Polygonum*	Sect. *Polygonum*	Sect. *Polygonum* subsect. *Polygonum*
Sect. *Pseudomollia*	—	Sect. *Pseudomollia*	Sect. *Polygonum*	Sect. *Pseudomollia*
Sect. *Duravia*	Sect. *Polygonum*	Sect. *Duravia*	Sect. *Polygonum*	Sect. *Duravia* subsect. *Duravia*
Sect. *Tephis*	—	Sect. *Tephis*	Sect. *Tephis*	Sect. *Polygonum* subsect. *Tephis*
Polygonella, *Gonopyrum*	*Polygonella* subg. *Polygonella*	*Polygonella*	*Polygonella* subg. *Polygonella*	Sect. *Duravia* subsect. *Polygonella*
Thysanella	*Polygonella* subg. *Thysanella*	—	*Polygonella* subg. *Thysanella*	Sect. *Duravia* subsect. *Polygonella*

ferent fields. The limits between the sections *Pseudomollia*, *Tephis*, *Duravia*, and *Polygonum*, relative to *Polygonella*, are also studied and clarified.

Material and Methods

A number of representative species of *Polygonella*, and species from all sections of *Polygonum* s. str., including sections *Duravia*, *Tephis*, *Pseudomollia*, and *Polygonum*, have been investigated. Material was either fixed in the field in FAA or removed from herbarium sheets. The origin of material is listed in Appendix 1. We studied selected characters considered to have systematic value based on previous studies, viz. pollen (Hedberg, 1946), fruit anatomy and surface patterns (Marek, 1954, 1958; Wolf & McNeill, 1986; Ronse De Craene et al., 2000), tepal epidermal structure (Ronse De Craene & Akeroyd, 1988; Hong et al., 1998), and gross floral morphology (Ronse De Craene & Akeroyd, 1988).

For LM observations herbarium material was either boiled in water or treated with sulfosuccinic acid 1,4-bis ester sodium salt (aerosol-OT: Ayensu, 1967). Flowers were first washed in a warm 10% KOH solution, before a treatment with Stockwell's bleach was applied to remove the excess of tannins (Schmid, 1977). Next material was run through an ethanol-tertiary butanol series and embedded in paraplast, sectioned at about 12 μm, and stained with saffranin and fast-green. The vasculature of a number of flowers was also studied after treatment with warm 10% KOH and clearing with lactic acid (Sporne, 1948).

Of the fruit wall only the exocarp (epidermis) survives at maturity and is usually lignified. As the cells are square, rectangular, or cylindrical they have the same shape in cross or longitudinal section. However, tangential (paradermal) sections can vary from the epidermis toward the mesocarp. In surface view the cells may be puzzle piece- to star-shaped, and become polygonal deeper within the tissue (see also Ronse De Craene et al., 2000).

For SEM observations herbarium material was treated with aerosol-OT, stored in 70% alcohol (Erbar, 1995), and dissected before treatment with dimethoxymethane (Gerstberger & Leins, 1978) and critical-point drying. SEM observations were carried out either with a Jeol 6400 scanning electron microscope (LV) or Zeiss DSM 962 (E) at 5–15 kV.

We also studied a number of observable macromorphological features of leaf, stem, inflorescence, and mature flowers and fruits, such as the overall shape of the flower, the shape of the tepals, tepal venation, the number of stamens and the filament shape, the number of carpels, and shape of the fruits. These characters were added to the micromorphological characters to perform a cladistic analysis comprising 51 characters and 25 species (including one subspecies) (see Appendices 3, 4). Parsimony analysis was performed with PAUP* version 4.0 (Swofford, 1998).

Fallopia cilinodis (Michx.) Holub was used as outgroup, and characters were unordered and all had equal weight. *Polygonum molliaeforme* was initially included in the analysis, but was later removed because of strong morphological convergences (see discussion). Parsimony analysis was performed using a heuristic search with TBR swapping and the steepest descent option. Relative support for clades was assessed with a 50% majority-rule bootstrap and jackknife analysis.

Table 2. Diagnostic characters used to separate *Polygonella* and different sections of *Polygonum* (based on Graham, 1958; Haraldson, 1978; Hickman, 1984; Horton, 1963; Lousley & Kent, 1981; Mitchell & Dean, 1978; Ronse De Craene & Akeroyd, 1988; Small, 1897; Watson, 1873; Wheeler, 1938).

	Polygonella	*Polygonum* sect. *Duravia*	*Polygonum* sect. *Polygonum*	*Polygonum* sect. *Pseudomollia*	*Polygonum* sect. *Tephis*
Number of flowers per unit	1	1(2–4)-flowered fascicles	often (1–)2–3(–6)-flowered fascicles	ochrea usually enclosing 1(2) flowers on each node	several flowers per node
Branch position	appearing internodal through adnation	nodal	nodal	nodal	nodal
Pedicel orientation	often curved	curved or erect	erect	erect	erect
Flower sex	bisexual/unisexual	bisexual	bisexual	bisexual	bisexual
Style fusion	separate to the base	separate to the base (*Duravia*) or fused at base (*Monticola*)	separate to the base, or fused below middle	fused ca. 0.1 mm from the base, and divided into two	fused at the base
Beak	present	present or absent	absent or weakly developed	present	present
Number of carpels	3, rarely 2(4)	3	2–3	2	2
Fruit wall	smooth to shallowly pitted	smooth, (shallowly) pitted or tubercled, rarely reticulate	conspicuously tubercled or smooth	pitted (reticulate), more strongly at the wings (also tubercles)	smooth to shallowly pitted
Number of stamens	8	5–8	5–8	6	(5–)6–7
Filament shape	inner abruptly dilated, rarely progressively so	inner progressively dilated	inner progressively dilated	inner progressively dilated	inner progressively dilated
Inner/outer tepals	strongly differing from each other in size and shape, outer often smaller than inner and flattened	not differing, or outer slightly longer and keeled with cucullate tips	not differing, or outer incurved, inner flat, outer sometimes cucullate or keeled	outer angular to keeled, not differing in size	outer keeled, not differing in size
Tepal accrescence	inner distinctly to slightly accrescent	not to slightly accrescent	not accrescent	not accrescent	not accrescent
Achene	included in perianth, rarely exserted	included in perianth	included to often exserted above perianth	included in perianth	included in perianth
Chromosome numbers	$N < 20$	$N < 20$, $N \geq 20$	$N < 20$, $N \geq 20$	unknown	unknown

Observations

Macromorphology of the flower (figs. 1, 2)

All tepals are similar in size and shape (Figs. 1D, 2C, D, F), or the outer tepals differ strongly from the inner ones (Fig. 1A, C, E). In some cases shape and size of tepals became increasingly different after anthesis. Outer tepals were found to be angular to keeled in species of sections *Polygonum*, *Duravia*, and *Tephis* (Figs. 1A, E, 2D). In section *Polygonum* the fruit tends to outgrow the perianth in size as to become increasingly exserted, and the tepals become appressed to the fruit. In sections *Tephis*, *Duravia*, and *Polygonella* the perianth loosely encloses the fruit, often becoming accrescent. A distinctive characteristic of some species of *Polygonella* (e.g., *Polygonella americana*, *Polygonella polygama*) is that the outer tepals become reflexed and are smaller than the accrescent inner ones (Fig. 1C).

The vasculature of the tepals is only rarely trifid (e.g., *Polygonum afromontanum*; Fig. 1A). In most cases it consists of a single dendritically branching vein (as a main trunk with short secondary ramifications along the trunk: most species of section *Polygonum* and some of section *Duravia*; Fig. 1B, D). In *Polygonella*, *Polygonum molliaeforme*, and some species of section *Duravia* there is only a single non-branching vein, or ramifications are few (Fig. 1C, E).

The most common arrangement of the stamens in the pentamerous Polygonaceae is of four equal stamens in two pairs opposite the two outer tepals, two unequal stamens opposite the intermediate tepal (one belonging to the inner whorl and one to the outer whorl), and single stamens opposite the two inner tepals (Fig. 1B, C; see, e.g., Laubengayer, 1937; Vautier, 1949; Ronse De Craene & Smets, 1991). Flowers are occasionally trimerous with six tepals (Fig. 1D). The transitional tepals have an intermediate shape and size (Figs. 1A, B, 2C, E) or are sometimes abnormally shaped (Fig. 1D). A single stamen is often found in sections *Tephis* and *Polygonum molliaeforme* instead of the usual stamen pair (Fig. 1A, E). Anthers are occasionally sterile, as in *Polygonum ramosissimum* (see also Ronse De Craene & Akeroyd, 1988). In all taxa studied the filaments of the inner stamens are inflated toward the base (Figs. 1A–E, 2A–E). In most species, the inflation is basipetally progressive from the middle of the filament, but in most species of *Polygonella* the filament abruptly widens in the lower half (Figs. 1C, 2A). However, this is not the case in *Polygonella fimbriata*, and its outer filaments are rarely inflated and are sometimes reduced (Horton, 1963). Nectar tissue is confined to the base of the inner filaments and extends onto the hypanthium surrounding the ovary. The nectary is not clearly visible, except for the epidermis that is not cutinized. Since no nectarostomata are visible, diffusion of nectar must take place through the non-thickened cell wall (cf. Ronse De Craene & Smets, 1991). Only in one species, *Polygonella articulata*, did we observe an apparently glandular rim (nectary?) of tissue surrounding the base of the gynoecium (see also Horton, 1963). For more details on nectaries in Polygonaceae we refer to Ronse De Craene and Smets (1991).

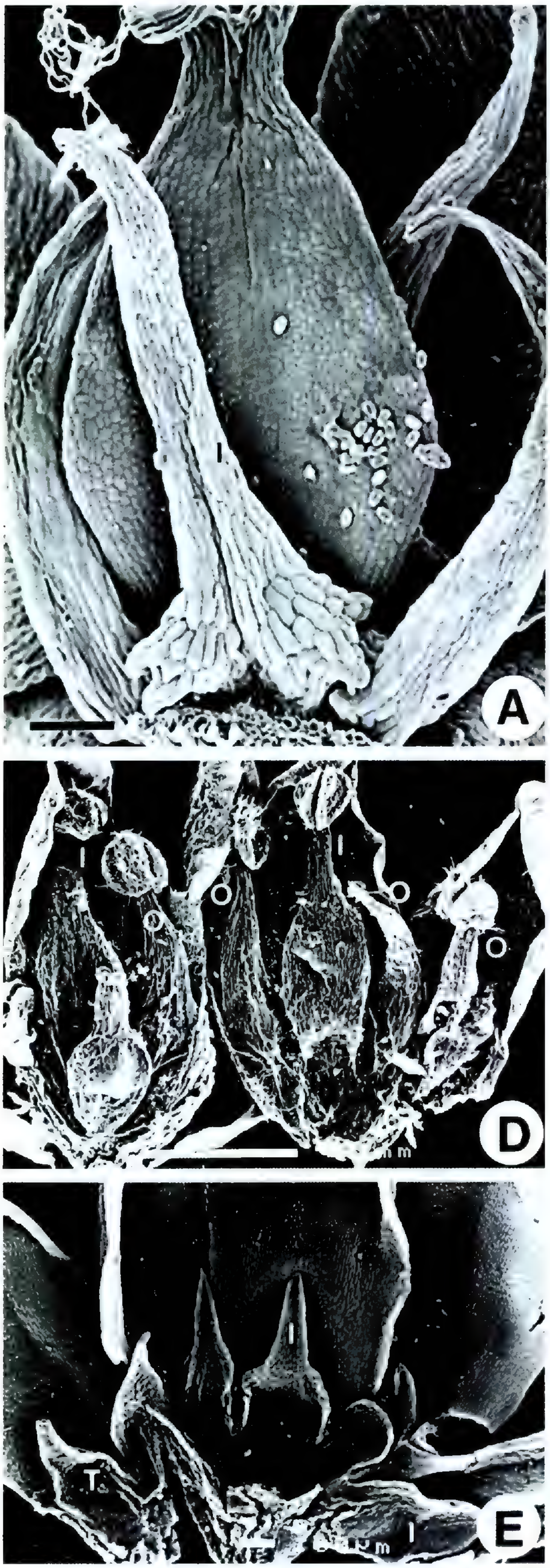
The shape of the gynoecium is either trigonous (three carpels) or lenticular (two carpels), and the fruit develops as an achene or nut. A condition with two carpels is consistently found in sections *Pseudomollia* (Fig. 6C) and *Tephis*, rarely in section *Polygonum*, and is almost absent in section *Duravia* and *Polygonella*. This may correspond with the loss of the intermediate tepal with accompanying stamens (Fig. 2D). Other differences between individual species exist in the presence (Figs. 6A, 7C, D) versus absence (Figs. 6C, 7A, B, F) of a basal stipe, the prolongation of the distal portion (beak) of the achene (Fig. 7C–F), as well as the development of the fruit angles or ribs (Figs. 6A, B, 7B, D, F). Fruits of *Polygonella* and several species of section *Duravia* are typically slender, triangular-ovoid with well-developed angles, stipitate, and beaked (Fig. 7C, D, F), although this is not always consistently so (Fig. 7A, E). The fruit of *Polygonum molliaeforme* is distinctive by the presence of a winged beak (Fig. 6C), although the wings may be variably developed. In section *Polygonum* the fruit is often disymmetric in transection, as two ribs are more prolonged compared to the third (Fig. 6B), or the opposite occurs (Fig. 2F).

Pollen morphology (figs. 3, 4)

In all genera and sections investigated the pollen is prolate to spheroidal and tricolporate (Polar axis/Equatorial diameter = 1.11–1.68). The ektexine is the most variable feature, and is either reticulate (Fig. 3B–F, H, I), tectate (smooth and spinulose: Fig. 3A), or rough (Fig. 3G). In species with a reticulate exine, usually the area surrounding the colpi features smaller lumina than seen in the polar and intercolpal area.

Species of *Polygonum* sect. *Polygonum* and section *Tephis* (*Avicularia*-type sensu Hedberg, 1946) consistently have tricolporate, rarely hexa-pantocolporate (= hexarugate), prolate-spheroidal grains with the exine surfaces smooth with spinules (Figs.

Figure 1. Floral shapes and structures, with flowers spread open and gynoecium removed (O, outer stamen; I, inner stamen; T, transitional stamen). —A. Section *Tephis*: *Polygonum afromontanum* (*Danish-Ethiopian Bot. Exped. 1622*). —B. Section *Duravia*: *Polygonum douglasii* (*Rydberg & Bessey 5364*). —C. *Polygonella polygama* (*Godfrey 1046*). —D. Section *Polygonum*: *Polygonum aviculare* (*Ronse De Craene 25 Lb*). —E. Section *Pseudomollia*: *Polygonum molliaeforme* (*Bornmüller 8181*). A, bar = 0.6 mm; B, C = 0.5 mm; D = 0.3 mm; E = 0.4 mm.



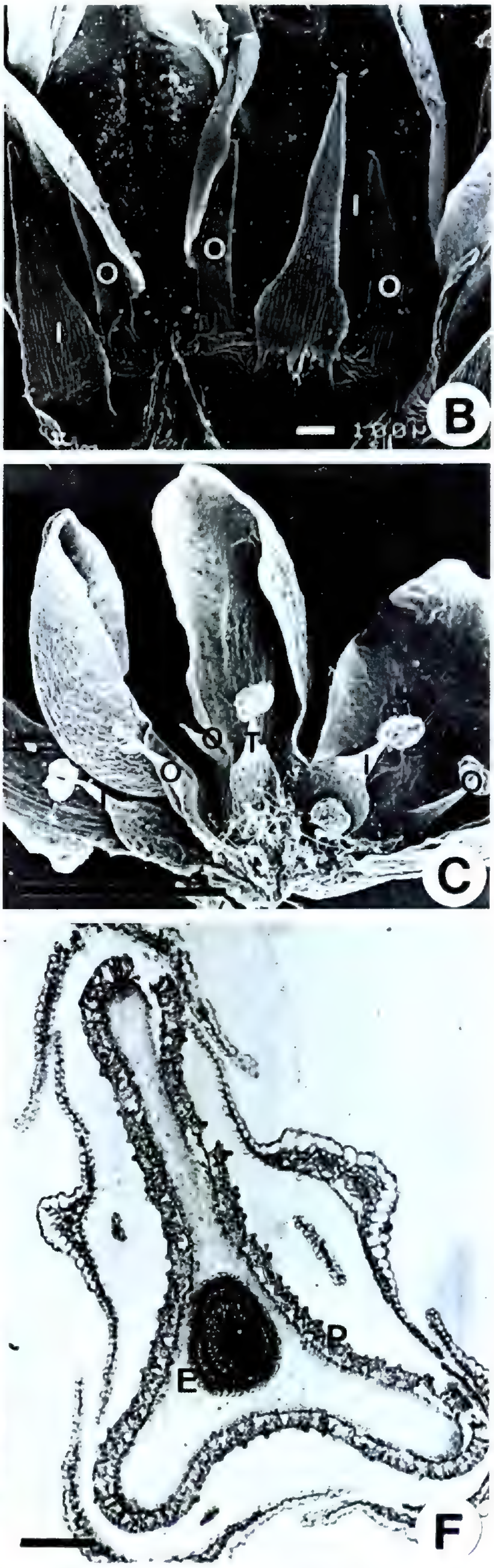


Figure 2. Flowers of *Polygonum* and *Polygonella*. SEM micrographs—A. *Polygonella parksii*: stamens and gynoecium; one inner tepal removed (*Correll & Correll 36649*). —B. *Polygonum californicum*: flower spread open (*Jepson s.n.*). —C. *Polygonum tenue*: flower spread open (*Puissant s.n.*). —D. *Polygonum undulatum*: flower spread open (*Fourcade 5962*). —E. *Polygonum aviculare*: flower spread open (*Ronse De Craene 25 Lb*). —F. *Polygonum aviculare:* transverse section of flower (*Ronse De Craene 25 Lb*). (E, embryo; I, inner stamen; O, outer stamen; P, pericarp; T, transitional stamen). Bars = 100 μm, except C, D = 1 mm.

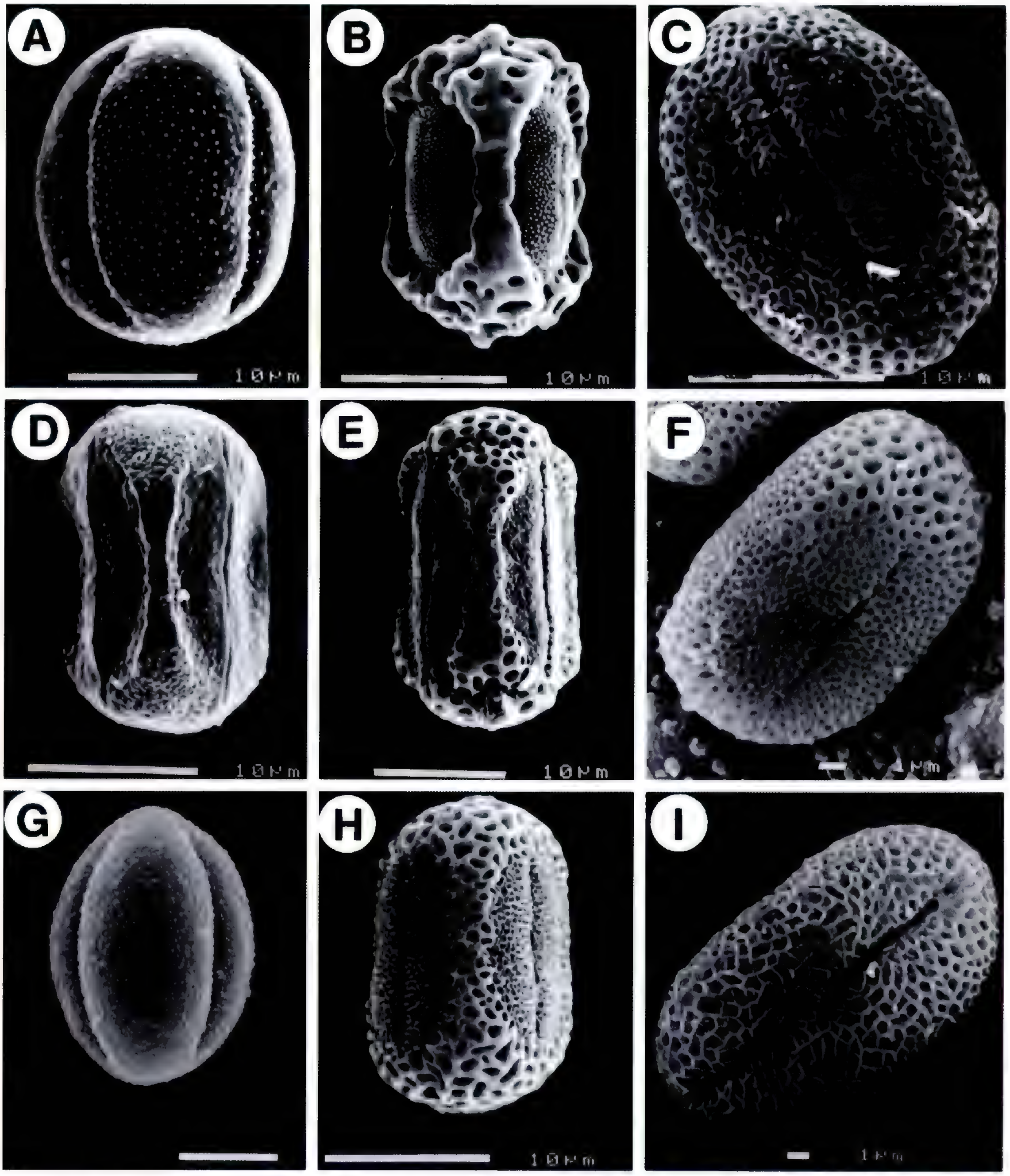


Figure 3. Equatorial view of pollen grains of *Polygonum* and *Polygonella*, SEM micrographs. —A. *Polygonum aviculare* (*Nanfeldt 15203*). —B. *Polygonum californicum* (*Jepson s.n.*). —C. *Polygonum douglasii* var. *latifolium* (*Howell s.n.*). —D. *Polygonum molliaeforme* (*Kotschy 778*). —E. *Polygonella americana* (*Fischer 10*). —F. *Polygonum tenue* (*Puissant s.n.*). —G. *Polygonum afromontanum* (*Hedberg 4320*). —H. *Polygonum minimum* (*Sandberg & Leiberg 799*). —I. *Polygonella polygama* (*Godfrey 1046*). Bars = 10 µm.

3A, 4A). In *Polygonum afromontanum* the exine surface is more or less roughened although comparable with section *Polygonum* (Figs. 3G, 4A).

Pollen of section *Pseudomollia* is tricolporate, prolate, and nearly triangular in polar view (Figs. 3D, 4D). It differs strongly from section *Polygonum* in its dimorphic exine, verrucose on both poles and mesocolpium, but mostly psilate around the ectoaperture (Figs. 3D, 4D).

Several species of *Polygonella* (Fig. 3E) and of *Polygonum* sect. *Duravia* (Figs. 3B, 3H, 4B) have tricolporate, prolate grains with a dimorphic exine (*Duravia*-type sensu Hedberg, 1946). The exine is semitectate-reticulate at the mesocolpium and the

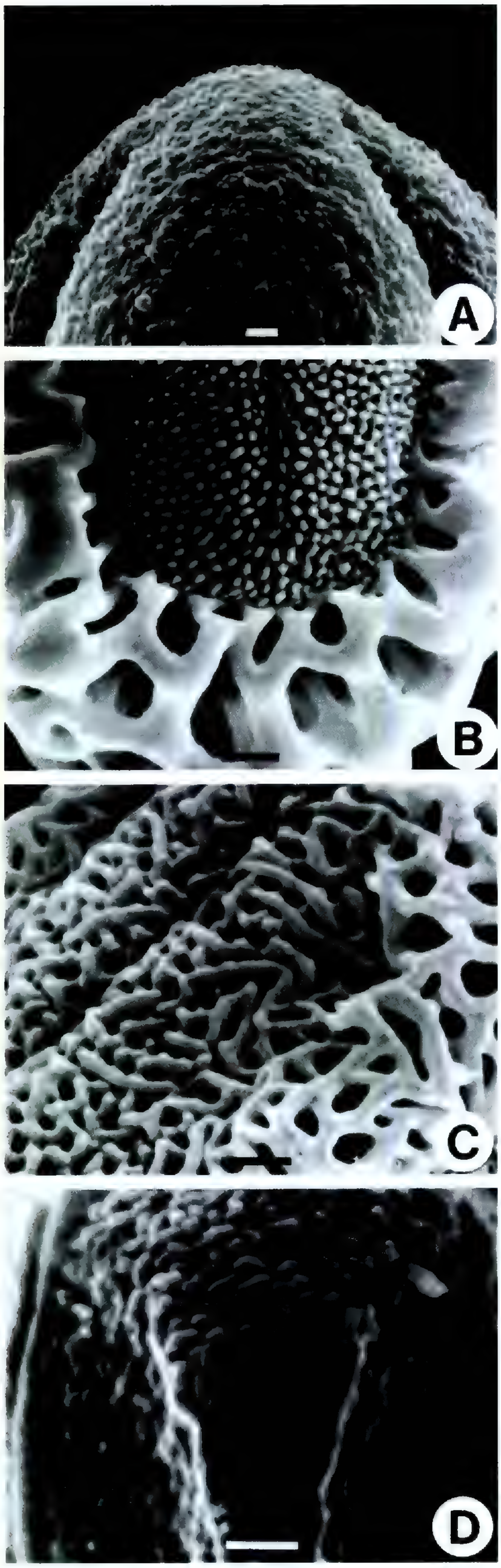


Figure 4. Details of ektexine of selected pollen grains of *Polygonum*, SEM micrographs. —A. *P. afromontanum* subsp. *soboliferum*: polar view (*Hedberg 4320*). —B. *P. californicum*: detail of alveoli and mesocolpium (*Jepson s.n.*). —C. *P. minimum*: detail of alveoli around colpus (*Sandberg & Leiberg 799*). —D. *P. molliaeforme*: detail of mesocolpium at pole and alveoli (*Kotschy 778*). Bar = 1 μm.

poles, and rugulate/reticulate or sometimes foveolate with microspinules around the ectoapertures. For some (e.g., *Polygonella polygama, Polygonella articulata, Polygonum douglasii, Polygonum minimum*: Figs. 3C, F, I, 4C), the difference between the exine surface at the mesocolpium and the ectoapertures is a minor question of size, and is in some cases not distinguishable (Fig. 3I). Homogeneously distributed lumina are found in some *Polygonella* (Fig. 3I). As this difference increases, more typical *Duravia*-types occur (e.g., *Polygonum californicum, Polygonella parksii, Polygonella americana*: Fig. 3B, E). The distinction between zones of reticulations may be abrupt (*Polygonum bolanderi*) or progressive (*Polygonum tenue:* Fig. 3F). It is thus possible to construct a progressive transformation series between the typical *Duravia*-type with strict boundaries between the mesocolpal area and the ectoapertural area and strictly reticulate pollen with only a slight difference between these zones.

EPIDERMAL CELLS OF THE TEPALS (FIG. 5)

The adaxial epidermis of the inner tepals was analyzed by Hong et al. (1998). We add more observations here that are in agreement with the previous results. Tepal epidermal characters cannot be used to differentiate *Polygonum* s. str. from *Polygonella* (cf. Hong et al., 1998). Two types of epidermal cells can additionally be distinguished herein (Fig. 5): more or less rectangular with straight anticlinal walls (Fig. 5D), or puzzle piece-shaped to rectangular outlines with undulate anticlinal walls (Fig. 5A–C, E). Cuticular striae are mostly deep and randomly distributed, but sometimes aligned in one direction.

FRUIT MORPHOLOGY AND ANATOMY (FIGS. 6–9)

The value of fruit anatomy in Polygonaceae was recognized previously (e.g., Lonay, 1922; Marek, 1954, 1958; Neubauer, 1971) and has been used by us recently to delimit the tribes Polygoneae and Persicarieae (Ronse De Craene et al., 2000). Two parameters have been recognized as taxonomically significant: (1) fruit surface patterns (with SEM) (Figs. 6–8), and (2) pericarp anatomy (with SEM and LM) (Fig. 9).

A single bitegmic seed develops from an orthotropous basal ovule and becomes surrounded by a hardened pericarp. The pericarp consists of a sclerified exocarp, a mesocarp, and endocarp (see also Lonay, 1922; Marek, 1958; Neubauer, 1971; Ronse De Craene et al., 2000). The thickenings most commonly occur on the anticlinal (radial) walls, but not

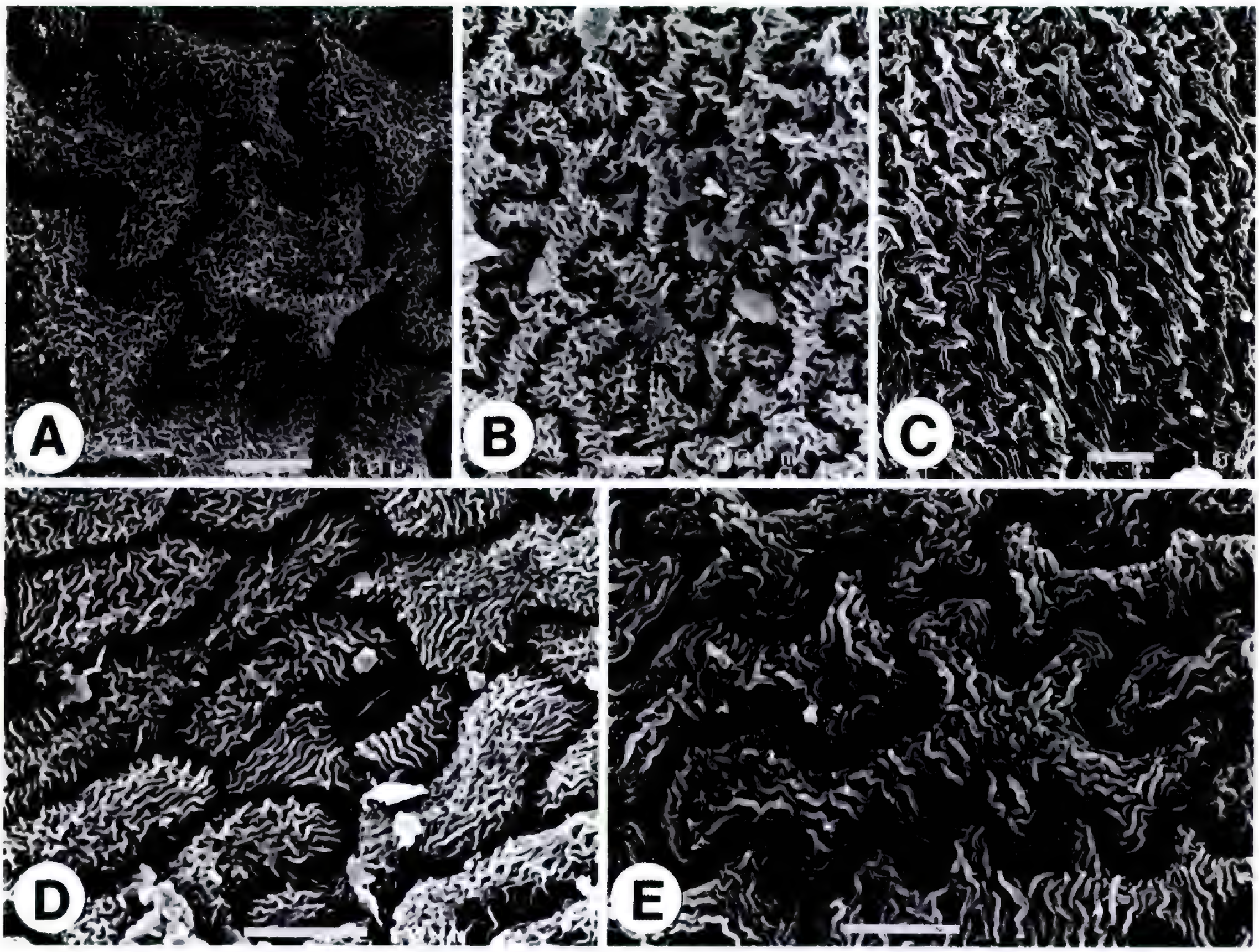


Figure 5. SEM micrographs of the inner tepal epidermis. —A. *Polygonella parksii* (*Correll & Correll 36649*). —B. *Polygonum douglasii* subsp. *spergulariiforme* (*Lyal 1858*). —C. *Polygonum bolanderi* (*Pringle s.n.*). —D. *Polygonum arenastrum* (*Ronse De Craene 1157*). —E. *Polygonum douglasii* var. *latifolium* (*Howell s.n.*). Bars = 10 μm.

on the inner tangential (periclinal) walls. As thickening of the anticlinal walls increases from the inner tangential wall to the outer, the lumen often takes a triangular to trapezoid shape in section (Fig. 9B, E, F). In other instances the thickenings are more regular and the lumen appears narrowly rectangular (Fig. 9A, C, H, I). Very often small canals branch from the lumen into the surrounding sclerenchymatous tissue (Fig. 9A, B, H, I). Due to space constraints the anticlinal walls can become variously convoluted or bent in cross or longitudinal sections (Fig. 9A, G, I). As convolutions of the anticlinal walls may also occur tangentially, this gives the cells a star- or puzzle piece-shape in surface view or in paradermal section, or the cell appears polygonal if no convolutions occur. Shifts in shape may occur within the cells from the periphery to the mesocarp (cf. Lonay, 1922). The outer surface of the epidermis represents interesting systematic characters, as emphasized by Marek (1954, 1958), Wolf and McNeill (1986), and Ronse De Craene et al. (2000).

In *Polygonella* the outer fruit surface is smooth (*Polygonella gracilis, Polygonella americana*: Fig. 7E, F), or with shallow pits (*Polygonella articulata*: Fig. 8I). Longitudinal cuticular striae are often present (Fig. 8I), but not in *Polygonella fimbriata* (Figs. 7D, 8H), or in *Polygonella gracilis*. *Polygonella fimbriata* has a mixture of a closely packed layer of "tubercles" on the upper fruit with a roughly pitted lower surface (Figs. 7D, 8H). Smooth surfaces are also found in *Polygonum* sect. *Duravia* (e.g., *Polygonum minimum*: Fig. 7A, *Polygonum paronychia*), and section *Polygonum* (e.g., *Polygonum maritimum*: Fig. 6A). In other species the upper half of the fruit can be tubercled and the lower half smooth (e.g., *Polygonum oxyspermum* subsp. *raii, Polygonum arenastrum*), and this is related with the pressure of the tepals at the base of the fruit. Smooth surfaces with pits representing the collapsed anticlinal walls of the cells were found in sections *Tephis* (Fig. 8G), *Pseudomollia*, and *Duravia* (e.g., *Polygonum shastense, Polygonum californicum*: Fig. 8D, *Polygonum coarctatum*, and *Polygonum tenue:* Fig. 8E). The fruit surface of *Polygonum polygaloides* s.l. (including subspecies

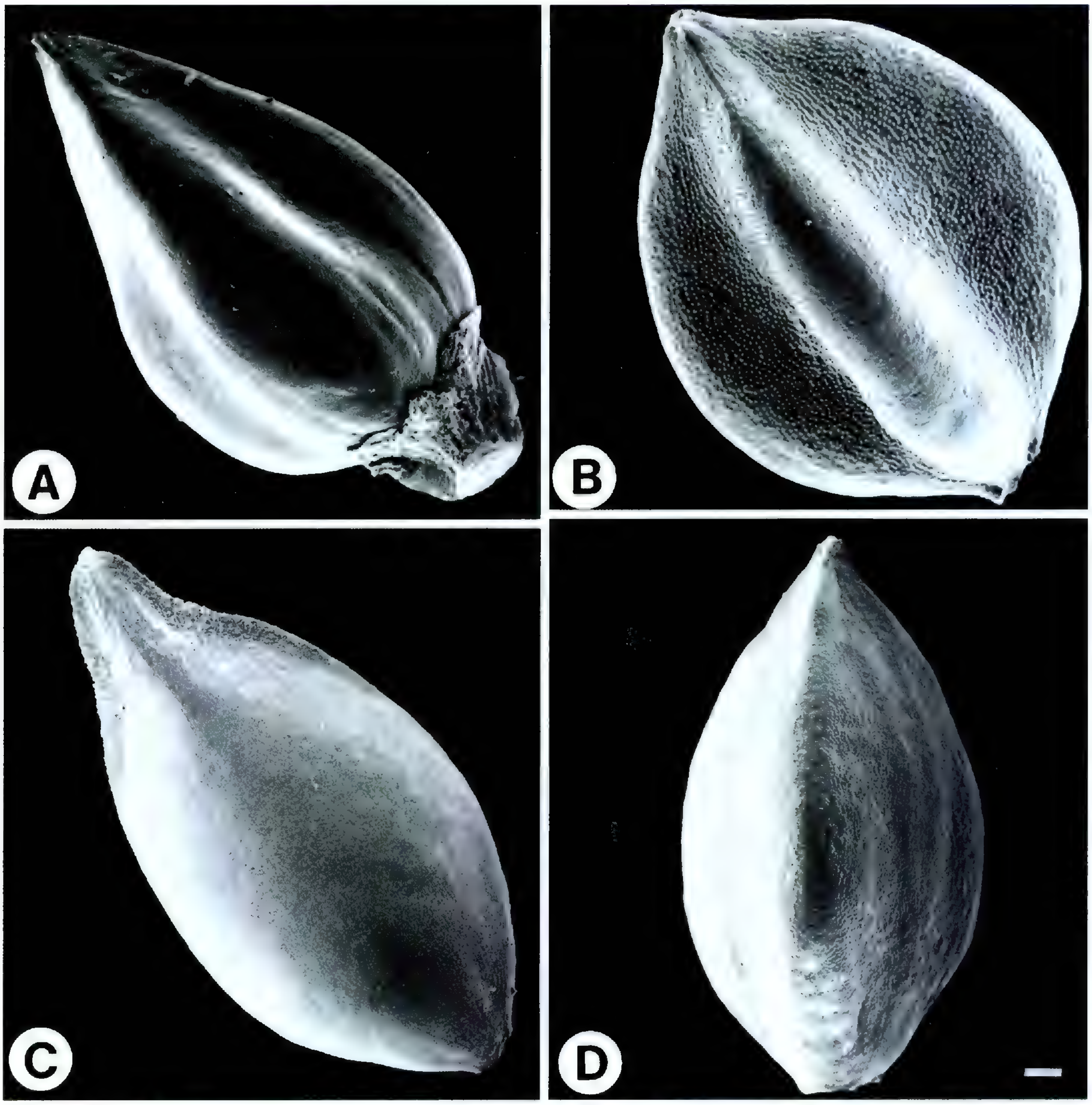


Figure 6. SEM micrographs of lateral views of entire fruits of *Polygonum* sects. *Polygonum*, *Molliaeforme*, and *Tephis* (tepals removed). —A. *P. maritimum*: smooth surface (*Nordin 102*). —B. *P. bellardii*: tubercled surface (*Heldreich 877*). —C. *P. molliaeforme*: foveate with short apical wings (*Kotschy 778*). —D. *P. afromontanum*: pitted surface (*Hedberg 4320*). Bar = 100 μm.

kelloggii: Fig. 8F; subspecies *confertiflorum*: Fig. 7C) is unique and shows a scalariform-reticulate pattern with longitudinally running ridges bridged at regular intervals with variations depending on the samples or subspecies studied. These ridges do not necessarily correspond with the anticlinal walls of the cells.

Several species of section *Polygonum* and a few of section *Duravia* have a distinct surface pattern covered by tubercles. Tubercles may be equidistant and sparsely covering the fruit along the anticlinal walls of the cells (e.g., *Polygonum bellardii*: Figs. 6B, 8A), crowded on ridges formed by the anticlinal cell walls (e.g., *Polygonum achoreum*, *Polygonum equisetiforme*: Fig. 8C), or in longitudinal rows or clusters without connection to the anticlinal walls of the cells (e.g., *Polygonum arenastrum*, *Polygonum aviculare*, *Polygonum douglasii*: Figs. 7B, 8B). Tubercles may be associated with pits, but never with superficial striae. *Polygonum douglasii* and *Polygonum tenue* differ markedly from most other species of section *Duravia* in the presence of tubercles arranged in short longitudinally placed rows (Fig. 8B). In some cases fruits with smooth-pitted surfaces and with globular emergences occur side by side in the same species (e.g., *Polygonum arenastrum*, *Polygonum douglasii*, *Polygonum spergulariforme*, *Polygonum kelloggii*, *Polygonum ten-*

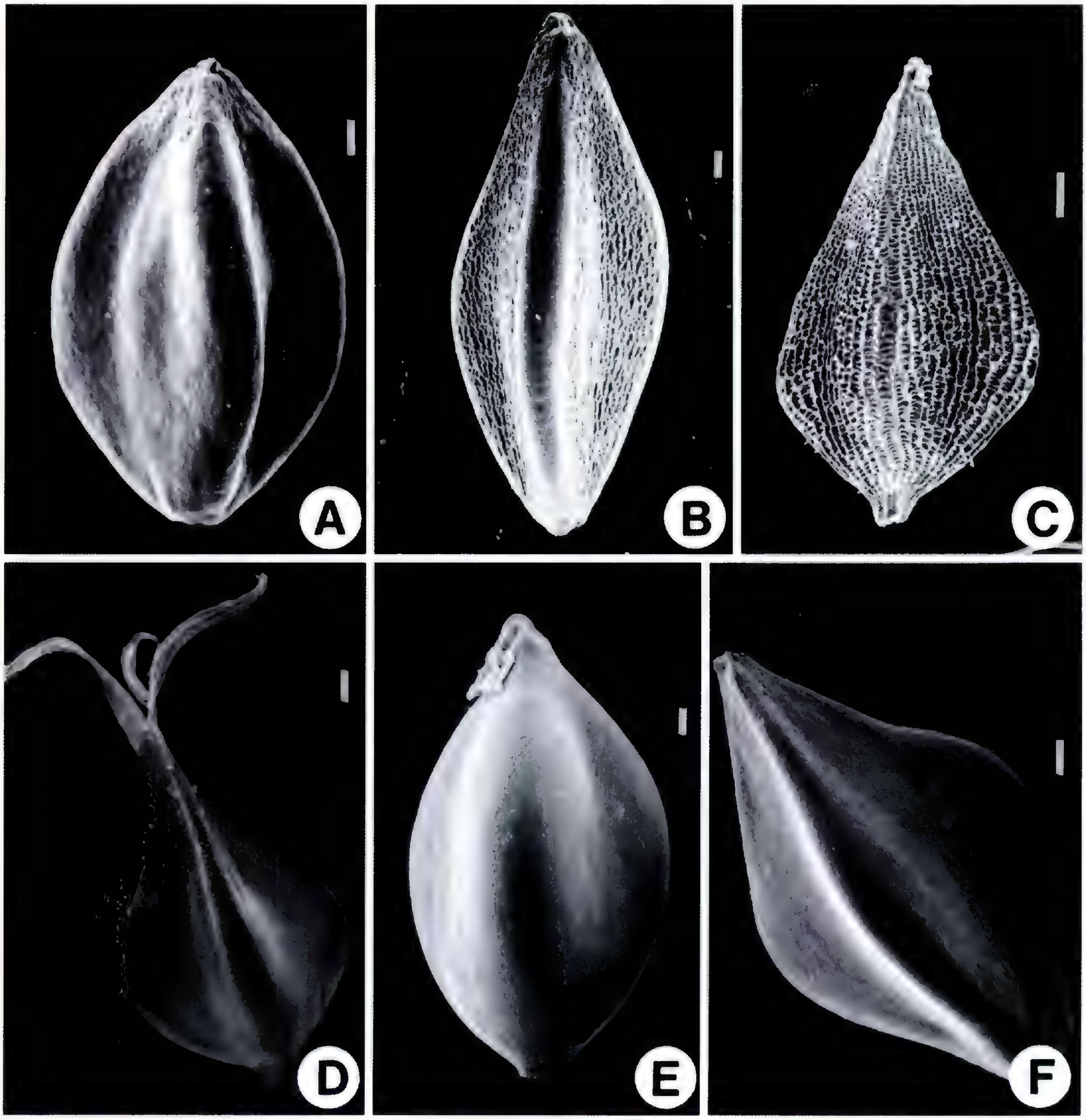


Figure 7. SEM micrographs of lateral views of fruits of *Polygonum* sect. *Duravia* and *Polygonella*. —A. *Polygonum minimum*: smooth surface (*Sandberg & Leiberg 799*). —B. *Polygonum douglasii*: tubercled surface (*Porter & Porter 9722*). —C. *Polygonum polygaloides* subsp. *confertiflorum*: reticulate surface (*Bacigalupi & Smith 5982*). —D. *Polygonella fimbriata*: smooth surface, apically pitted (*Blanton 6825*). —E. *Polygonella gracilis*: smooth surface (*Vestulund s.n.*). —F. *Polygonella americana*: smooth to pitted surface (*Fischer 10*). Bars = 10 μm.

ue: Fig. 8E). The lenticular fruit of *Polygonum molliaeforme* (sect. *Pseudomollia*) is distinctive with a roughly reticulate surface and deep pitting along the wings lining the beak of the fruit (Fig. 6C); the reticulation is more compact and is covered with tubercles at some places (see also Ronse De Craene et al., 2000). The extent of development of the angles of the fruit is correlated with a different surface pattern between the ribs and the angles. In some species this difference is well pronounced (e.g., *Polygonella fimbriata, Polygonum molliaeforme*: Figs. 6C, 7D, 8H).

Sections of the fruit have been made for a representative number of species (for details see also Ronse De Craene et al., 2000). In LS the exocarp consists of palisade-like cells (20–80 μm thick) with slightly undulate or straight radial walls. In section *Polygonum* the radial walls appear convolute because of irregular thickening on the inner wall (Lonay, 1922; Neubauer, 1971). The lumen of the cells is narrowly rectangular with dendritical branching toward the outer tangential wall (Fig. 9A, C). The wall is usually thick (> 60 μm) but sometimes thinner (< 40 μm as in *Polygonum oxysper-*

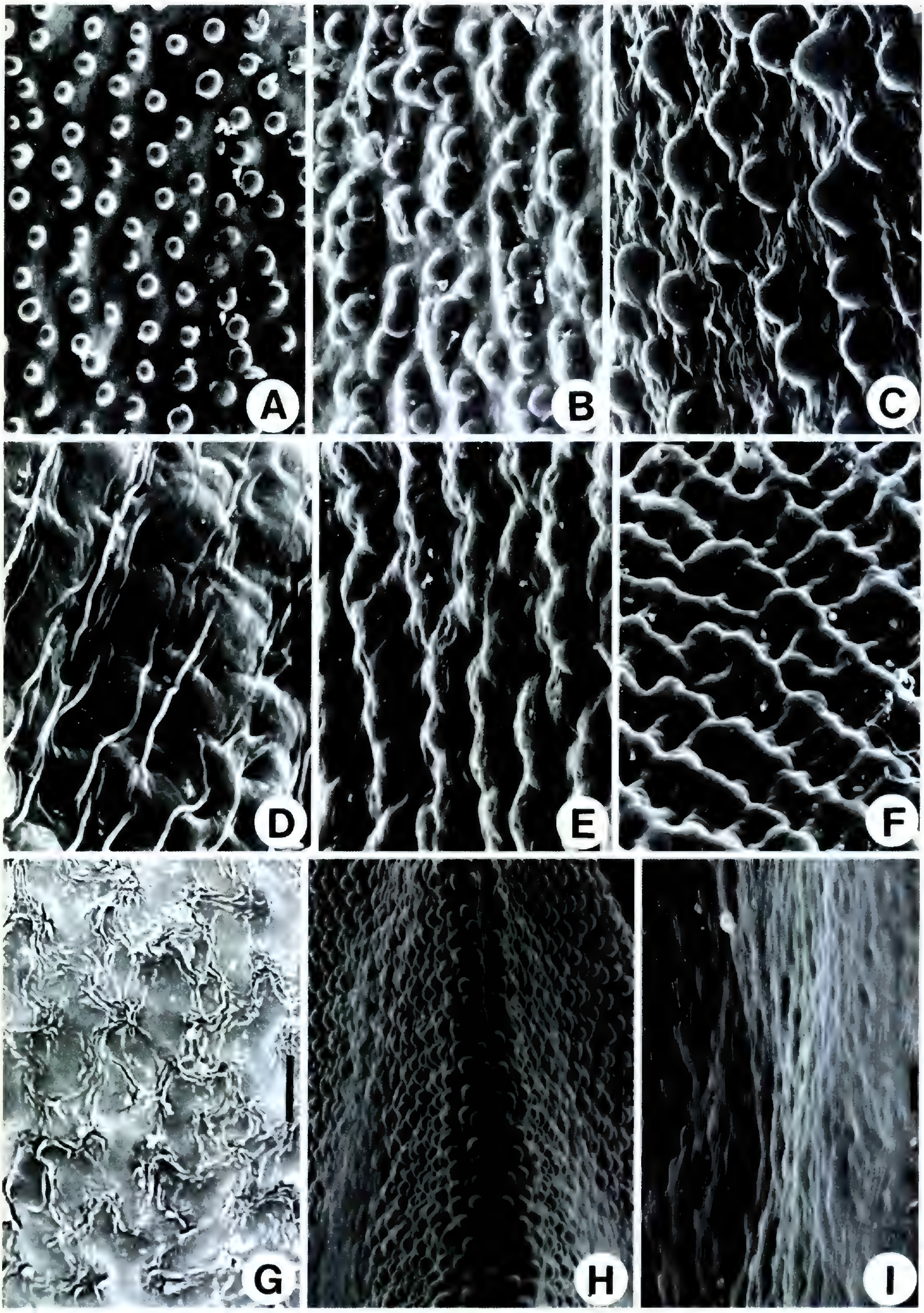


Figure 8. SEM micrographs with details of fruit surfaces of *Polygonum* and *Polygonella*. —A. *Polygonum bellardii*: tuberculed (*Heldreich 877*). —B. *Polygonum douglasii*: tubercles in clusters (*Porter & Porter 9722*). —C. *Polygonum equisetiforme*: tubercles with pits (*Ronse De Craene 975*). —D. *Polygonum californicum*: smooth to pitted surface with striae (*Jepson s.n.*). —E. *Polygonum tenue*: pitted surface (*Puissant s.n.*). —F. *Polygonum polygaloides* subsp. *kelloggii*: reticulate surface (*Porter & Porter 7555*). —G. *Polygonum undulatum* (*Fourcade 5962*): smooth with pits. —H. *Polygonella fimbriata*: detail of granular rib (*Blanton 6825*). —I. *Polygonella articulata*: pitted surface with striae (*Bodin s.n.*). Bars = 10 μm, except A and I = 100 μm.

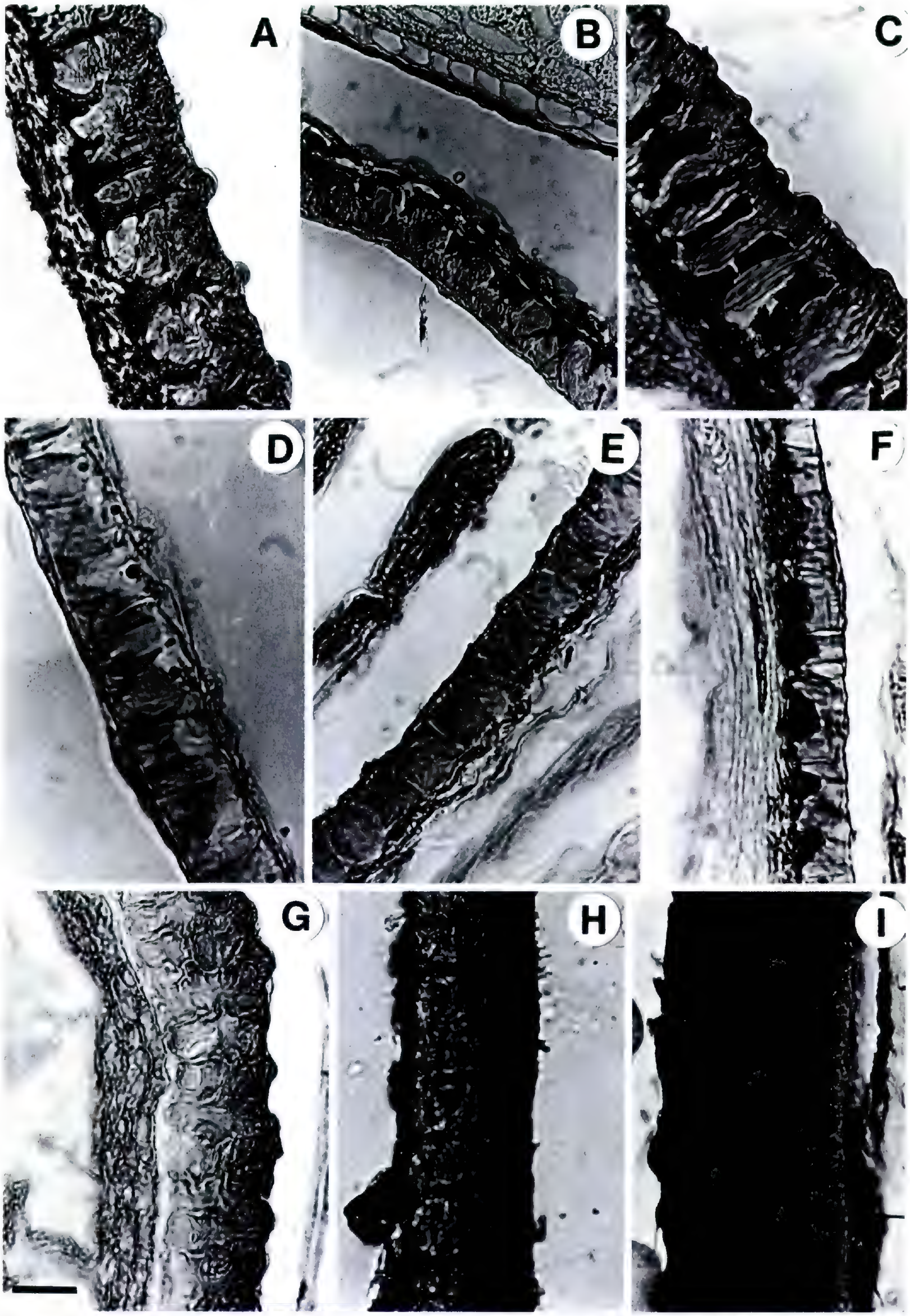


Figure 9. LM micrographs of transverse and longisections of pericarps of *Polygonum* and *Polygonella*. —A. *Polygonum ramosissimum* (*Puissant s.n.*), TS. Bar = 35 μm. —B. *Polygonum oxyspermum* subsp. *raii*. (*Corbière 5306*), TS. Bar = 70 μm. —C. *Polygonum bellardii* (*Heldreich 877*), TS. Bar = 30 μm. —D. *Polygonum shastense* (*Carpenter s.n.*), LS. Bar = 20 μm. —E. *Polygonella polygama* (*Curtiss s.n.*), LS. Bar = 15 μm. —F. *Polygonum molliaeforme* (*Kotschy 778*), LS. Bar = 10 μm. —G. *Polygonum afromontanum* (*Hedberg 377*), TS. Bar = 40 μm. —H. *Polygonella americana* (*Fischer 10*), TS. Bar = 20 μm. —I. *Polygonum tenue* (*Greene s.n.*), LS. Bar = 20 μm.

mum subsp. *raii*: Fig. 9B). More or less similar wall structures were observed in species of section *Duravia* (e.g., *Polygonum douglasii, Polygonum tenue*: Fig. 9I), section *Tephis* (although the convolution is more important and it lacks the dendritical branching: Fig. 9G), and only rarely in *Polygonella* (e.g., *Polygonella americana:* Fig. 9H). Almost straight radial walls (< 40 μm wide) with narrow lumina occur in other species of section *Duravia* (e.g., *Polygonum coarctatum, Polygonum shastense, Polygonum californicum*: Fig. 9D), most *Polygonella* (e.g., *Polygonella articulata, Polygonella polygama*: Fig. 9E), and in section *Pseudomollia* (Fig. 9F). Here the lumen appears narrowly rectangular, x-shaped to triangular with the broad base on the inner tangential wall. Dendritical canals are not observed. As emphasized elsewhere (Ronse De Craene et al., 2000), there is no link between the shape of the exocarp cells and the outer surface of the fruit.

Cladistic Analysis

The cladistic analysis resulted in 108 trees of length 179 (consistency index (CI) 0.402, retention index (RI) 0.640). The consensus tree is shown in Figure 10 and the 50% majority-rule consensus tree with bootstrap and jackknife values in Figure 11. As is evident from Figures 10 and 11, the trees obtained are relatively well supported (given that all characters used were morphological). Two major clades can be recognized, one containing all species of section *Duravia* and the genus *Polygonella* with a bootstrap-jackknife support of 67%/70%, and another weakly supported clade (BS 64/59%) containing sections *Polygonum* and *Tephis*. In preliminary analyses *Polygonum molliaeforme* consistently fell within section *Duravia*, probably because of convergences in morphological characters, and was consecutively removed from the analysis. The greatest internal support is for the group of species recognized as *Polygonum polygaloides* and allied species (cf. Hickman, 1984, BS 92%). Two clades remain strongly supported within the *Polygonum* clade (sect. *Tephis*) and a clade of three species (*Polygonum arenastrum, Polygonum maritimum, Polygonum oxyspermum*). The 50% majority-rule consensus tree shows the collapse of internal branches in both clades. Species of *Polygonella* form three paraphyletic clades with species of *Polygonum* sect. *Duravia*, although two of the clades are well supported. Synapomorphies can be recognized for both clades, such as the presence of spinules and ochrea morphology in the *Polygonum* clade, and the *Duravia*-type of pollen and P/E index (except for one species) in the *Duravia* clade.

Discussion

We found little unambiguous evidence to support a full segregation of the genus *Polygonella*, because several features known to be distinctive of the taxon appear regularly in *Polygonum*, especially in section *Duravia*. If the genus *Polygonella* is considered as sufficiently distinct, a number of species from *Polygonum* sect. *Duravia* would have to be transferred to *Polygonella*. This would considerably reduce the number of characters necessary to distinguish *Polygonella* as a genus, unless other evidence is found. Typical *Polygonella* species show the following features: a single flower per node arising from the axil of a short scaly bract, a tendency for unisexuality in some species, flowers often pendulous with the abscission zone in the middle of the pedicel, perianth mostly unequal with shorter often reflexed outer tepals, and inner tepal lobes mostly larger, accrescent, and not appressed to the fruit. Tepal venation is reduced to a single midvein. The number of stamens is usually not reduced, and the inner filaments are abruptly widened. The pollen has a well-marked dimorphism of the ektexine. Fruits are slender-stipitate and are often beaked; the surface is smooth, mostly with striae, and pericarp cells have a narrow lumen without dendritical branching and straight radial walls. However, as shown in Table 2 and Appendix 4, the differences between *Polygonella* and the other tribes are not straightforward. There are a few general characteristics for the species of *Polygonella*, although these are not shared by all, except for the scarious bracts, internodal branches, and the pedicel abscission zone. The cladistic analysis based on morphological characters does not permit the identification of a well supported *Polygonella* clade with these characters (Figs. 10, 11). Therefore, we cannot ascertain that these are synapomorphies.

Vautier (1949) and Horton (1963) interpreted the presence of a single unbranched vein as a reductive feature. Flowers of *Polygonella* (with tepals having an average length of 3 mm, even becoming accrescent in fruit) are not necessarily smaller than those of *Polygonum* s. str. It can be speculated that the reduction in tepal vein may be an adaptation to an arid environment necessitating less water transport. Some *Polygonum* growing in similar dry habitats also have a single unbranched vein (e.g., *Polygonum molliaeforme*: Fig. 1E).

The exine of pollen of section *Duravia* and *Po-*

Strict consensus of 108 trees

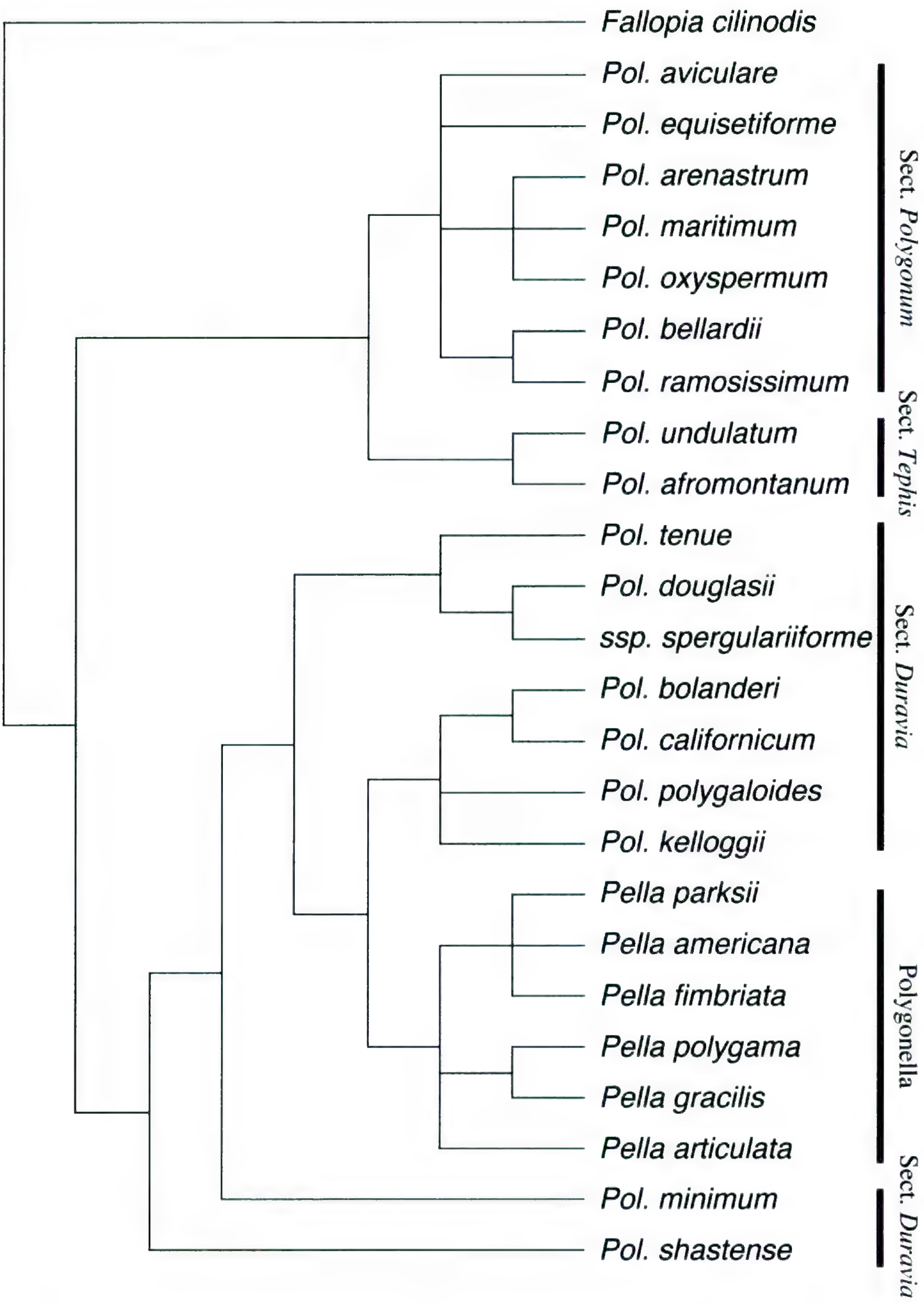


Figure 10. Strict consensus of 108 trees (length 179, CI 0.402, RI 0.640). Pol. = *Polygonum*; Pella = *Polygonella*.

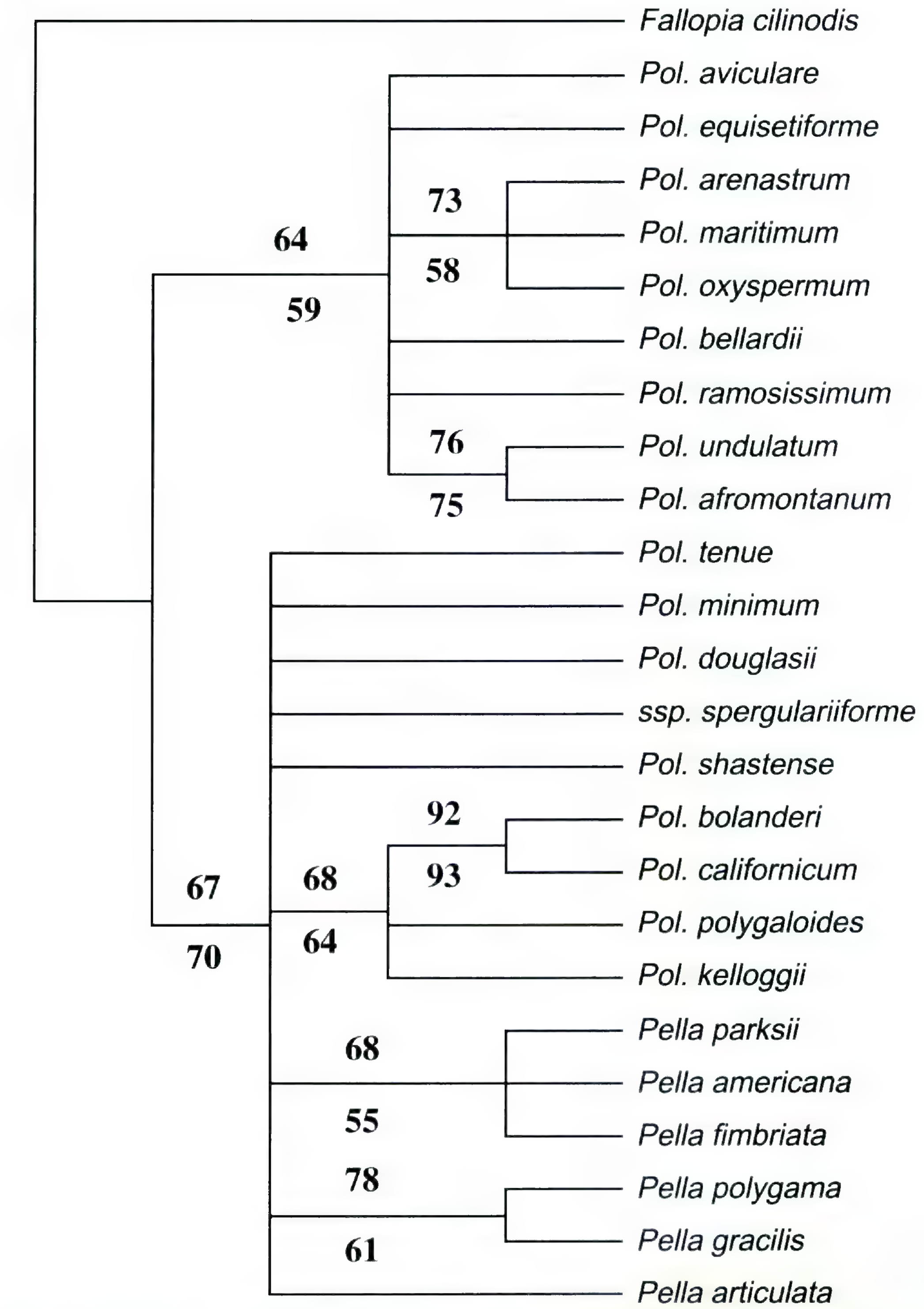


Figure 11. Bootstrap and jackknife 50% majority-rule consensus tree. Bootstrap values shown above branches, jackknife values below. Pol. = *Polygonum*; Pella = *Polygonella*.

lygonella appears to have a mixture of the pattern in *Persicaria* (an alveolate reticulum) and section *Polygonum* (a finely granular surface surrounding the furrows; see also Hedberg, 1946; Nowicke & Skvarla, 1977; Hong & Oh, unpublished). Hedberg (1946) argued that the similarities in pollen of *Polygonella* and section *Duravia* are the result of convergent evolution, because of differences in habit, a disjunct geographical distribution, and the repetition of the transition between the *Duravia*-type and *Avicularia*-type within the *Polygonella* group. Pollen of section *Polygonum* is invariably smooth with scattered microspinules, and there is little or no variation in this pattern. The *Avicularia*-type of pollen can be readily recognized and differs from the reticulate pollen found in some species of section *Duravia* and *Polygonella*, a fact not recognized by Hedberg. There are strong indications that the similarity in pollen morphology of section *Duravia* and *Polygonella* reflects a synapomorphy for both taxa. Regarding the structure of the exine one has a clear continuum of variation in the pollen of section *Duravia* and *Polygonella*. On one extreme, the pollen of *Polygonella polygama* and some *Polygonum douglasii* is reticulate-alveolate without dimorphism (Fig. 3I). A slight differentiation of the size of the reticulate pattern between the mesocolpium/poles and ectoapertures is found in *Polygonum tenue* (Fig. 3F) and *Polygonum douglasii* (var. *latifolium*; Fig. 3C). This difference is more pronounced in pollen of *Polygonum minimum* (Figs. 3H, 4C), *Polygonum douglasii* subsp. *spergulariiforme*, *Polygonum shastense*, *Polygonella parksii*, *Polygonella articulata*, and *Polygonella fimbriata* with a reticulate-rugulate pattern. A change in the pattern of sculpturing around the ectopores occurs in *Polygonum californicum* by the presence of microspinules above the reticulation (Figs. 3B, 4B). The area around the ectoapertures can also become psilate to foveolate without traces of a reticulation (Fig. 3E).

However, no clear link can be made between the smooth exine with microspinules of *Polygonum* sect. *Polygonum* (Fig. 3A), and the reticulate-alveolate pattern of *Polygonella* and *Polygonum* sect. *Duravia* (Fig. 3B, C, E, F, H, I). This distinction supports the recognition of section *Duravia* separate from section *Polygonum*. The pollen differences between *Polygonella* and section *Duravia* are almost inexistent, and the two are clearly interrelated.

Interestingly, the pollen of *Polygonum molliaeforme* of section *Pseudomollia* appears as intermediate between the *Avicularia*- and the *Duravia*-type (Hong & Oh, unpublished). Given the disjunct geographical distribution of section *Pseudomollia* in Iran and section *Duravia* in North America, it is probable that a dimorphic exine has arisen independently and more than once. Moreover, some species of *Fallopia*, another genus of tribe Polygoneae (e.g., *F. convolvulus*, *F. scandens*, *F. dumetorum*: Ronse De Craene, unpublished), also show a dimorphic exine (viz. a smooth mesocolpium but punctate in the region of the colpi), as rightly pointed out by Nowicke and Skvarla (1977). Indeed, we found that two pollen types occur side by side between different species of *Fallopia* (Hong et al., unpublished), viz. with a dimorphic exine or a more uniform one.

By observing fruit surface patterns with the SEM we could distinguish three main types: (1) smooth, possibly with small pits; (2) with globular protuberances (tubercles), lined along the anticlinal walls of the cells, or aggregate in rows; (3) with interconnected ridges separated by depressions (reticulate). In addition, longitudinal striae may be present and may be weakly or strongly developed. Wolf and McNeill (1986) recognized four surface patterns for species of section *Polygonum* occurring in Canada: smooth, roughened, papillose, and striate-papillose. A distinction between smooth and roughened achenes appears to be related to the collapse of the anticlinal cell walls. The papillose and striate-papillose types correspond with the types we described as tubercled. The value of surface patterns appears to be mostly restricted to the specific level in section *Polygonum*, with the occasional presence of smooth achenes and achenes having tubercles (e.g., *Polygonum arenastrum*, *Polygonum douglasii*, *Polygonum tenue*, *Polygonum ramosissimum*).

While we found highly distinctive surface patterns in some species, the different sections could not be delimited solely on the basis of the fruit surface, as different types overlap between the sections. There is also an intergradation between different patterns, with a smooth surface at one extreme, and the highly distinctive tubercled surface at the other. Stages in between are a rough surface with shallow to deep pits, and with widely spaced to aggregated tubercles.

There is strong overlap between some species of section *Duravia* and section *Polygonum* on the one hand, and between section *Duravia* and *Polygonella* on the other. Similar smooth fruit surfaces (possibly with pits lining the anticlinal cell walls) are found in *Polygonum* sect. *Duravia* (e.g., *Polygonum californicum*, *Polygonum minimum*) and section *Polygonum* (e.g., *Polygonum maritimum*). The slender stipitate fruits of typical species of *Polygonella* with smooth-striate surface (Fig. 7D, F) can be often recognized in species of section *Duravia*

(Fig. 7B, C). In contrast, other species of section *Duravia* have a pattern more similar to *Polygonum* sect. *Polygonum* (*Polygonum douglasii*: Fig. 8B, *Polygonum tenue*: Fig. 8E). The reticulate pattern of *Polygonum polygaloides* and allies (Fig. 8F) appears as a completely divergent type, possibly derived from a pitted surface as in *Polygonum tenue*. Smooth and tubercled surfaces can occur side by side in closely related species, or even within the same species. *Polygonella fimbriata* has its fruit partly covered with tubercles (Fig. 8H).

Sections of exocarps revealed two main patterns, which were not necessarily linked with the external fruit surface: (1) broadly square to cylindrical cells (> 50 μm) with strongly convolute radial walls, broad lumen and dendritical branching toward the periphery; (2) narrowly rectangular cells (< 40 μm) with straight radial walls, narrow lumen, and absence of dendritical branching.

The internal fruit wall in *Polygonum* sect. *Pseudomollia* resembles that of *Polygonella* to a great extent in lacking dendritical canals, and with straight radial walls and narrow lumen (Fig. 9F). This pattern also occurs in species of section *Duravia* centered around *Polygonum californicum*.

The presence of strongly convolute radial walls correlates with a tubercled surface (rarely smooth) and an absence of striae. All studied species of sections *Polygonum* (Fig. 9A–C) and *Tephis* (Fig. 9G) show this characteristic pattern, as well as some species of section *Duravia* (*Polygonum douglasii*, *Polygonum tenue*: Fig. 9I). *Polygonella americana* is an obvious exception for the genus with its convolute radial walls (Fig. 9H).

Can *Polygonella* Be Maintained as a Genus Separate from *Polygonum*?

Polygonum s.l. has always been difficult from a taxonomic point of view, and several attempts have been made in the past to improve the infrageneric limits (see Ronse De Craene & Akeroyd, 1988, for an overview). In contrast, *Polygonella* has always been considered as distinct, first close to *Atraphaxis*, then in the vicinity of *Polygonum* s. str. (Table 1). This study, however, has demonstrated that *Polygonum* s. str. and *Polygonella* share several characters that were thought to be distinctive, and that a strict taxonomic separation at the generic level is not tenable.

Based on the present study the following conclusions are significant:

(1) Strict delimitation between *Polygonella* and *Polygonum* s. str. is not supported. Characters of several species of *Polygonum* sect. *Duravia* overlap with those of *Polygonella*. *Polygonum* sect. *Duravia* appears paraphyletic relative to *Polygonella*, with a basal position for the polymorphic *Polygonum douglasii*.

Especially on the basis of pollen (the distinctive *Duravia*-type of pollen and the reticulate exine), as well as fruit anatomy (rectangular cells with straight radial walls and more or less triangular lumen), a separation of section *Duravia* from section *Polygonum*, and including *Polygonella*, is best maintained. Polymorphic species, such as *Polygonum douglasii*, can have different characters spread over different populations. For example, *Howell s.n.* (ex *Wibbe 7841*), *Carpenter s.n.*, and *Porter & Porter 9722* have a tubercled fruit surface and a thick pericarp; *Howell s.n.* (ex *Wibbe 7842*) has a smooth surface with a thin pericarp. Similarly, pollen of *Polygonum douglasii* subsp. *spergulariiforme* strongly resembles the *Duravia*-type, while the other samples of *Polygonum douglasii* studied are intermediate with little differentiation between mesocolpium and colpi regions. However, more research in these polymorphic groups is clearly needed. Also, the sampling for this study is too limited to draw definite conclusions about the interspecific relationships of section *Duravia*.

(2) *Polygonum* sect. *Tephis* cannot be well separated from section *Polygonum*. Both sections share similar pollen morphology, fruit surface patterns, and fruit anatomy. Distinctive features are the afromontane distribution and dimerous flowers of section *Tephis*.

The pollen with rough exine with microspinules and the roughly pitted fruit surface of *Polygonum afromontanum* (Figs. 3G, 4A, 6D) is found in several species of section *Polygonum*. Similarities with *Polygonum undulatum* are even greater. Ronse De Craene and Akeroyd (1988), however, maintained the section, mainly because of dimerous flowers with keeled outer tepals, and the development of two lateral veins on the tepals. Stamen number is also six in *Polygonum afromontanum* (with 5 tepals) and *Polygonum undulatum* (with 4 tepals), the two outer not being "duplicated," as in *Polygonum molliaeforme* (numbers may vary between 6 and 8). In *Polygonum undulatum*, the perianth is dimerous, apparently by the loss of an outer tepal with two stamens. The dilated inner filaments and tepal epidermis (Hong et al., 1998) match those of section *Polygonum*. However, the inclusion of anatomical characters may support a subsectional rank. Given the limited geographical distribution, this could also be justified.

(3) *Polygonum* sect. *Pseudomollia* is distinctive in external fruit characters (winged lenticular achenes),

but shows overlap in characters of pollen and fruit anatomy with *Polygonella*. These are probably the result of convergences. The different phytogeography (the former occurs in Persia, while the latter is restricted to North America) supports this.

Section *Pseudomollia* Boiss. was originally erected on the basis of the lenticular achene with two-parted style, solitary flowers, and overlapping ochreae. Material investigated by Ronse De Craene and Akeroyd (1988) had only five stamens, as the outer were not "duplicated"; another specimen missed one outer pair altogether. Haraldson (1978) mentioned the presence of five stamens and two or three staminodes; these probably represent the outer stamens. Rechinger and Schiman-Czeika (1968) mentioned 5 to 8 stamens and suggested that anthers drop off easily, which might give the false impression of staminodes. The reduction of outer stamens and the inflated filament bases, coupled with one unbranched vein per tepal, as well as the tepal epidermal cells (Hong et al., 1998) fit within section *Polygonum*. Haraldson (1978) did not find the anatomical differences important enough to merit sectional rank. However, the fruit morphology (Fig. 6C) with lateral winglets along the beak is quite distinctive, as well as the pitted reticulate fruit surface. Also, the pollen with dimorphic exine and distinctive sculpturing is not matched in section *Polygonum*. The absence of secondary ramifications of the tepal veins is another distinctive feature, also found in *Polygonella* and some species of section *Duravia*. Given the extended proposal in this paper for delimiting the genus *Polygonum* s. str., *Pseudomollia* is best maintained as a section of *Polygonum*.

SECTIONAL AND SUBSECTIONAL DELIMITATION

Polygonella appears nested within a well-defined genus *Polygonum*. Characters shared by species of *Polygonum* have been listed in Ronse De Craene and Akeroyd (1988) and include the dilated inner filaments with occasional replacement of the outer stamen pair by single stamens, or their reduction, the absence of structural nectaries, similar tepal epidermal cells, the single vein per tepal, and the difference between outer and inner tepals. To reflect more natural monophyletic groupings, the merging of *Polygonella* within *Polygonum* is indicated and given below. Alternatively, the genus *Polygonella* could be maintained and expanded as to include all species of section *Duravia*. However, this shift is not advisable, as one cannot find sufficient diagnostic evidence to identify *Polygonella* as distinct from *Polygonum*, besides the pollen. Indeed, the maintenance of a generic status is exaggerated, compared to other genera such as *Fallopia*, *Persicaria*, and *Fagopyrum*. For example, the inclusion of the genus *Reynoutria* Houtt. as a section of *Fallopia* by Ronse De Craene and Akeroyd (1988) has been supported by cytological studies (e.g., Bailey & Stace, 1992). A similar logic is applied here for *Polygonella*. *Polygonella* may be viewed as an extreme evolutionary line within section *Duravia*.

Hickman (1984) proposed the rank of subgenus *Duravia* for the North American species of *Polygonum* (see introduction). We do not support this subdivision on the basis of a range of characters (the variation of *Polygonum polygaloides* falls within *Polygonella*). Two distinctive features characterize *Polygonella*: the abscission zone is situated in the middle of the pedicel, and the branches appear internodal by fusion with the main stem. *Polygonella* is best included within section *Duravia* of *Polygonum* s. str. The characters shared by this section are obvious: *Duravia*-type pollen (with all possible intermediates), a reduced number of flowers per inflorescence, a smooth fruit surface with narrow pericarp of rectangular cells (*P. polygaloides* has a distinctive outer surface), and a tendency for the outer tepals to become strongly dimorphic from the inner, with a single unsplit vein. A subdivision of a subsection *Thysanella* separate from *Polygonella* (as was done by Horton, 1963) appears superfluous as the differences enumerated for *Thysanella* are made irrelevant by the inclusion of species from section *Duravia* within *Polygonella*.

We propose the following sectional division for *Polygonum* sensu stricto:

Polygonum L. sect. **Polygonum**
Subsection **Polygonum** (L.) Ronse De Craene & S.-P. Hong, stat. nov. TYPE: *Polygonum aviculare* L.
Subsection **Tephis** (Adans.) Ronse De Craene & S.-P. Hong, stat. nov. TYPE: *Polygonum undulatum* (L.) Bergius = *Atraphaxis undulatum* L.

Polygonum sect. **Pseudomollia** Boiss. TYPE: *Polygonum molliaeforme* Boiss.

Polygonum sect. **Duravia** S. Watson
Subsection **Duravia** (S. Watson) Ronse De Craene & S.-P. Hong, stat. nov. TYPE: *Polygonum californicum* S. Watson
Subsection **Polygonella** (Michx.) Ronse Decraene. & S.-P. Hong, stat. nov. TYPE: *Polygonum articulatum* L.

A key to the sections and subsections is presented in Appendix 2.

We have shown that the notion of *Polygonella* as an independent genus should be abandoned. The results of this study reflect the need for a renewed investigation of the North American species of *Polygonum*. With a few exceptions no substantial molecular studies have been performed in the Polygonaceae, especially in the genus *Polygonum*. This would be a helpful addition to our morphological investigations. The understanding of the internal relationships of *Polygonella* to section *Duravia* could be highly improved, as our study does not clarify the internal relationship of the clade optimally.

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APPENDIX 1. Origin of species studied, with their synonymy. Species used in the cladistic analysis are marked with *.

● **Polygonum** sect. **Polygonum**

1. *Polygonum aviculare* L.*
SOUTH AFRICA. **Kimberley region:** Kalkdrift, *Brueckner 771* (UPS). BELGIUM. Bruges, subsp. *aequale*; pickled: *Ronse De Craene 25 Lb* (LV). SPAIN. **Malaga Prov.:** Fuengiola, *Nanfeldt 15203* (UPS) (pollen).
2. *Polygonum achoreum* Blake
U.S.A. **Wyoming:** Crook Co., Sundance, *Porter & Porter 8384* (UPS).
3. *Polygonum maritimum* L.*
FRANCE. **Bouches-du-Rhône:** Camargue, étang d'Iland, *Nordin 102* (UPS). GREECE. **Kos:** W of Tingakion, *Davis 67953* (E).
4. *Polygonum erectum* L.
U.S.A. **Illinois:** Fountaindale, *Bebb s.n.* (UPS). **Pennsylvania:** Delaware Co., 1 mi. NE of Broomall, *Wheeler 5660* (E).
5. *Polygonum bellardii* All.*
GREECE. **Thessaliae:** Pharsalum, *Heldreich 877*, ex Herb. *Bullemont 8369* (LV). HUNGARY: *Herb. De Dieudonné* (BR).
6. *Polygonum equisetiforme* Sibth. & Sm.*
TUNISIA. **Jerba:** near hotel Toumana, *Ronse De Craene 975* (spirit 309 Lt) (LV).
7. *Polygonum arenastrum* Boreau*
U.K. **Devon:** Prawle Point, E. Prawle, *Ronse De Craene 1157* (spirit 405 Le) (LV).
8. *Polygonum oxyspermum* Meyer & Bunge ex Ledeb. subsp. *raii* (Bab.) D. A. Webb & Chater *
FRANCE. **Manche:** Vauville et Denneville, *L. Corbière 5306*, ex Herb. *Bullemont 8443* (LV).
9. *Polygonum ramosissimum* Michx.*
U.S.A. **Kansas:** St. Mary's, *P. A. Puissant s.n.* (LV).

● **Polygonum** sect. **Tephis**

1. *Polygonum afromontanum* Greenway*
KENYA. **Nanyuki Distr.:** Mt. Kenya, NW slope along Sirimon, *Hedberg 4320* (UPS). ETHIOPIA. **Kaffa Prov.:** *Danish-Ethiopian Botanical Expedition 1972–1973 1622* (K). **S Bale Prov.:** Ririka, *Hedberg 377* (UPS).
2. *Polygonum undulatum* (L.) Bergius*
SOUTH AFRICA. **Humansdorp Distr.:** 2.6 mi. from Assegaai Bosch, *Fourcade 5962* (BOL). **Knysna:** in apertis Zitzikamma, *Schlechter 5974* (E).

● **Polygonum** sect. **Pseudomollia**

1. *Polygonum molliaeforme* Boiss.
IRAN. Kuh-Daena, *Kotschy 778* (UPS); Denawand, *Bornmüller 8181* (K); Kuh-Daena, *Kotschy s.n.* (type) (E).

● **Polygonum** sect. **Duravia**

1. *Polygonum californicum* Meisn.*
U.S.A. **California:** Butler Co., N of Oroville, *Heller 11763* (NY); Eal River, *Jepson s.n.* ex Herb. *Wibbe 92-7830* (LV); Eal River, viii 1892, *Jepson s.n.* (UPS) (pollen); Glen Co., 8 mi. E of Newville, *A. A. Heller 11553* (E).
2. *Polygonum polygaloides* Meisn.*
U.S.A. **Oregon:** *Howell s.n.* (LV); ex Herb. J. Wibbe,

T. Howell s.n. (BR). **Wyoming:** Uinta Co., Snake River, *Nelson & Nelson 6463* (UPS). **California:** Nez Percez Co., Lake Waha, *A. A. & E. G. Heller 3394* (E).
Subsp. *kelloggii** (E. Greene) Hickman [= *Polygonum kelloggii* Greene]: U.S.A. **Wyoming:** Johnson Co., Big Horn Range, W of Buffalo, Circle Park, *Porter & Porter 7555* (UPS).
Subsp. *confertiflorum** (Nutt. ex Piper) Hickman [= *Polygonum confertiflorum* Nutt. ex Piper]: U.S.A. **California:** Modoc Co., 9 mi. NW of Camby, *Bacigalupi & Smith 5982* (UPS). CANADA. **Saskatchewan:** Battle Creek, *Herb. Geological Survey of Canada 12890* (E).
3. *Polygonum shastense* Brewer*
U.S.A. **California:** E North Peak, *Nygsen s.n.* (UPS). **California?** Placer Co., *A. M. Carpenter s.n.* ex Herb. *Wibbe 92-7880* (LV); N slopes above Coldsham, Sierra Nevada, *C. F. Sonne s.n.* ex Herb. *Wibbe 92-7879* (LV).
4. *Polygonum tenue* Michx.*
U.S.A. **Massachusetts:** Milten Blue Hills, *Forbers 1346* (UPS); Baltic Co., *P. A. Puissant s.n.* (LV), *Greene s.n.* (UPS). **North Carolina:** Asha Co., bluff Mt., *Leonard et al. 2038* (E).
5. *Polygonum douglasii* E. Greene*
U.S.A. Placer Co., Sierra Nevada Mts., *A. M. Carpenter s.n.* ex Herb. *Wibbe 92-7840* (LV). **Wyoming:** Southern Carbon Co., W slope of Sierra Madre, *Porter & Porter 9722* (UPS). **Oregon:** base of Stein's mountain, *Howell s.n.*, ex Herb. *Wibbe 92-7841* (LV).
As var. *latifolium* E. Greene. U.S.A. **Oregon:** Siskiyou Mountains, *Howell s.n.*, ex Herb. *Wibbe 92-7842* (LV).
As *P. douglasii* greene var. *montanum* Small: U.S.A. **Montana:** Small, *Rydberg & Bessey 5364* (K). **Nevada:** Washol Co., Mt. Rose, Nevada agricultural Experiment Station Herbarium, *C. L. Brown s.n.* (E).
Subsp. *spergulariiforme** (Meisn. ex Small) Hickman [= *Polygonum coarctatum* Dougl. ex Meisn.]: U.S.A. **Oregon:** Grant's Pass, *Howell s.n.* ex Herb. *Wibbe 92-7881* (LV), *Lyal 1858* (K), *Lemmon 1210* (UPS). **California:** University of California Jepson Herb. (lectotype of *P. coarctatum*) (E); Trinity Co., Hettenshaw Valley, *S. K. Harris et al. 942* (E); Trinity Co., Van Duren River, 3 mi. below Hettenshaw valley, *S. K. Harris et al. s.n.* (E).
6. *Polygonum bolanderi* Brewer ex A. Gray*
U.S.A. **California:** Napa Hills, *C. G. Pringle s.n.*, ex Herb. *Wibbe 92-7829* (LV).
7. *Polygonum paronychia* Cham. & Schlecht.
U.S.A. **California:** San Francisco, Golden Gate Heights, *Rose 47103* (UPS).
8. *Polygonum minimum* S. Watson*
U.S.A. **Washington:** Cascades, Stevens Pass, *Sandberg & Leiberg 799* (BR, UPS). **Montana:** on trail to Sperry Glacier, *L. M. Umbach 823* (E).

• **Polygonella**
1. *Polygonella americana* (Fisch. & Mey.) Small*
U.S.A. **Texas:** Cat. Springs, *Fischer 10* (UPS). **Arkansas:** Hot Springs Co., Malvern, *Palmer 8473* (K). **Alabama:** Blount Co., Blackwarrior Creek, *Meisner 1845* (BR).
2. *Polygonella articulata* (L.) Meisn.*
U.S.A. **Massachusetts:** *Oakes? s.n.* (UPS). **New Jersey:** Woodbury, *Henry S. Conard s.n.* (LV); Middlesex Co., South Amboy, *Bodin s.n.* (UPS).
3. *Polygonella polygama* (Vent.) Engelm. & Gray [= *Polygonella parvifolia* Michx.]*
U.S.A. **North Carolina:** Brunswick Co., Orton Plantation Garden, *Godfrey 1046* (K). **California:** *Curtiss s.n.* (UPS). **Florida:** Indian River, *Curtiss 2433* (LV), *Curtiss 5525* (K); Palm Beach, *Curtiss 5525* (E).
4. *Polygonella parksii* Cory*
U.S.A. **Texas**: Leon Co., Normangle, Hilltop lakes resort, *Correll & Correll 36649* (K).
5. *Polygonella fimbriata* (Elliott) Horton*
U.S.A. **Florida:** Tampa, *Blanton 6825* (S).
6. *Polygonella gracilis* Meisn.*
U.S.A. **Mississippi:** Sandy barrens, Pass Christian, *A. B. Langlois 177*, ex Herb. *Wibbe 92-7817* (LV). **Florida:** Orange Co., Killarney, *O. Vestulund s.n.* (UPS).

APPENDIX 2. Key to (sub)sections of *Polygonum* sensu stricto.

1a. Flowers dimerous, fruits usually lenticular.
  2a. Small annual herbs, pollen dimorphic, fruit surface tubercled with lateral wings ..... sect. *Pseudomollia*
  2b. Small to large shrubs, pollen monomorphic (*Aviculatia*-type), fruit surface smooth to pitted ..... subsect. *Tephis*
1b. Flowers pentamerous, fruits usually trigonous.
  3a. Flowers borne in clusters of 2 to 4(6) per node, rarely with single flower per node, outer stamens occasionally reduced, pollen *Aviculatia*-type, tepal vasculature dendritical ..... subsect. *Polygonum*
  3b. Flowers borne singly on each node (rarely 2 or more), always with 8 stamens and three carpels, pollen *Duravia*-type or derived within, tepal vasculature dendritical or reduced to a single vein.
    4a. Bracts subtending individual flowers or flower clusters leaf-like with papery ochreolae, abscission zone when present just below flower ..... subsect. *Duravia*
    4b. Bracts subtending individual flower scarious, abscission zone in the middle of the pedicel ..... subsect. *Polygonella*

APPENDIX 3. Characters used in the cladistic analysis (based on pers. obs.; Meisner, 1826, 1857; Haraldson, 1978; Horton, 1963; Lousley & Kent, 1981; Mitchell & Dean, 1978; Ronse De Craene, 1986; Ronse De Craene & Akeroyd, 1988; Ross-Craig, 1979; Small, 1897; Watson, 1873; Webb & Chater, 1964; Wheeler, 1938; Wolf & McNeill, 1986)..

1. Habit: erect to ascending herbs, rarely shrubs (0), prostrate to creeping herbs (1), climbing herbs (2).
2. Leaf shape: ovate-cordate (0), ovate to lanceolate (1), narrowly lanceolate-linear (2).
3. Ochrea morphology: entire (0), two-cleft (1), lacerate (2).
4. Ochrea at maturity: entire (0), lacerate (1).
5. Leaf base: jointed with ochrea (0), not or obscurely so (1).
6. Awns on top of ochrea: absent (0), present (1).
7. Heterophylly: absent (0), present (1).
8. Internodal fusion of branches: absent (0), present (1).
9. Inflorescence: with numerous flowers/node (0), with 2 to 4(6) flowers/node (1), with 1(2) flowers/node (2).
10. Bracts of flowers: leaflike with pellucid ochreolae (0), scarious (1), scarious with awns (2).

11. Flowers exserted from ochreola: not (0), barely so (1), entirely (2).
12. Pedicel orientation at fruiting: erect (0), curved (1).
13. Abscission zone of flower: absent (0), against the base of the flower (1), in the middle of the pedicel (2).
14. Gender distribution: bisexual (0), unisexual—gynomonoecious or dioecious (1).
15. Differentiation of outer and inner tepals at fruiting (shape): subequal (0), slightly dimorphic (1), highly dimorphic (2).
16. Differentiation of outer and inner tepals at fruiting (size): subequal (0), outer smaller (1), inner smaller (2).
17. Division of perianth parts: below the middle (0), up to the middle (1).
18. Tepal venation: trifid (0), dendritical (1), only midvein (2).
19. Outer tepals at maturity: flattened (0), angular-cucculate (1), with a prominent keel (2).
20. Outer tepal orientation at fruiting: erect (0), reflexed (1).
21. Lateral walls of tepal epidermal cells: ± straight (0), strongly undulating (1).
22. Cuticular striations on tepal epidermal cells: random (0), in rows (1).
23. Stamen number: eight (0), occasionally less than eight (1), always less than eight (2).
24. Stamen reductions: eight stamens present (0), outer stamen pairs replaced by single stamen (1), outer stamen pairs partly incomplete (2), outer stamen pairs with sterile anthers or lost (3), inner stamens missing (4).
25. Filament shape of three inner stamens: not dilated or only at the base (0), gradually dilated toward the base (1), abruptly dilated in the middle (2).
26. Trichomes at the base of the filaments: present (0), absent (1).
27. Pollen size (polar axis length): small to medium, $<$ 25 μm (0), large, $\geq$ 25 μm (1).
28. P/E ratio (pollen size): 1.1–1.4 (0), 1.5–1.8 (1).
29. Apertural margins: absent (0), similar texture to the rest of the grain (1), different texture from the rest of the grain (2).
30. Ektexine differentiation: none (0), two distinct zones (1).
31. Mesocolpial ridges: not differentiated (0), strongly developed (1).
32. Pollen ektexine sculpturing pattern: smooth to rough perforate-punctate (0), foveolate to reticulate (1), baculate (2).
33. Pollen ektexine microspinules: absent (0), smooth (1).
34. Pollen type sensu Hedberg (1946): *Avicularia*-type (0), *Duravia*-type (1), other (2).
35. Presence of glandular rim around gynoecium: absent (0), present (1).
36. Merosity of flowers: trimerous (0), pentamerous (1), dimerous (2).
37. Number of carpels: three (0), two (1).
38. Occurrence of fruit dimorphism: absent (0), present at the same time (1), with a distinction between early- and late-season fruits (2).
39. Achene shape: broadly ovate ($L < 1.5W$) (0), intermediate ($L = 1.5–2W$) (1), lanceolate ($L > 2W$) (2).
40. Achene apex: without beak or with very short beak (0), with conspicuous to very long beak (1).
41. Stylar development: very short and equal in size to stigmatic lobes (0), two times as long as stigmatic lobes (1), $> 2\times$ stigmatic lobes (2).
42. Achene base: not stipitate or with very short stipe (0), conspicuously stipitate (1).
43. Achene shape in transection: subangular (0), with two convex and one concave side (1).
44. Achene covering by tepals: included (0), shortly exserted to 1/4 (1), strongly exserted above 1/4 (2).
45. Primary sculpturing pattern: smooth to inconspicuously pitted (0), with interrupted longitudinal ridges (1), with reticulate pattern (2).
46. Secondary sculpturing pattern: tubercules absent (0), present (1).
47. Longitudinal striations on achene: absent (0), present (1).
48. Radial walls of pericarp in longitudinal section: straight (0), convolute (1).
49. Thickness of pericarp in longitudinal section: $<$ 40 μm (0), $>$ 40 μm (1).
50. Shape of lumen of pericarp cells: broadly rectangular (0), narrowly rectangular (1).
51. Presence of dendritical canals in pericarp walls: absent (0), present (1).

Appendix 4. Data matrix for cladistic analysis. *Pol.* = *Polygonum*; *Pella* = *Polygonella*. [Exported from MacClade file]

	0 0 1 1 2 2 3 3 4 4 5 1 5 0 5 0 5 0 5 0 5 0
Fallopia_cilinodis	20000000121?000010001000000000102010000110000000111
Pol._aviculare	11110010?000100001000011111000001001?00101011101111
Pol._equisetiforme	11100000101010010000001100000001001?00010000101111
Pol._arenastrum	11110000?010100011000011110000001001020000 1?1?00001
Pol._maritimum	11110000101010000100000011000000100100000?10000001
Pol._oxyspermum	11110000102010000100000011000000100101010?0120?00001
Pol._bellardii	01110000 10?010000110100011000000100101010100?101111
Pol._ramosissimum	01110010?010101001101021110000001 00?020001?00101111
Pol._undulatum	011?000010?000000?100120111000001002 10?010011001111
Pol._afromontanum	01?10000?020?000002001 1?11100001100210 10?0000001 11?
Pol._tenue	0?010110?000100201001000110110120101011000 00??11111
Pol._minimum	?10000001020100201001 01?110110120101001?10010000001
Pol._douglasii	0?000100?021100001101000110010120101011001 00??01111
Pol._douglasii subsp. *spergulariiforme*	02000100?020100001101000110121120101010101 00??01001
Pol._shastense	?1000000?021100101010100111110120101002011010010010
Pol._bolanderi	02011000200010120?201100110121120101002 1??000000010
Pol._californicum	02011000200010120220100011112 11?010100212000001 0010
Pol._polygaloides	0?000000?000101202101112110110120101011121002000010
Pol._kelloggii	02000000200010120?101100110110120101011 10000?000010
Pella_parksii	02000111212 0??100200100021111012010100112000001????
Pella_polygama	01000001 21?021010201000021010002010100110101001 0000
Pella_americana	02000001 21?020210201000021112 11?010100111000001 1111
Pella_articulata	02000001212120020200100021011012011100110001001 0010
Pella_gracilis	01000001211121010200100021011012010100112 10?0000000
Pella_fimbriata	02000101 22?02?200200000011111012010100212 10?0101111

[Note that some polymorphic entries were converted to missing data, represented by ?]

POLLINATION BIOLOGY OF *ARISTOLOCHIA GRANDIFLORA* (ARISTOLOCHIACEAE) IN VERACRUZ, MEXICO[1]

K. S. Burgess,[2] J. Singfield,[2] V. Melendez,[3] and P. G. Kevan[4]

Abstract

The flowers of *Aristolochia grandiflora* are sapromyiophilous trap blossoms that deceive their visitors with optical and olfactory promise of hidden protein-rich substrate. The most effective pollinators are large Diptera, mostly Calliphoridae, which become trapped in the protogynous flowers on the first day of anthesis. Although the flowers are protogynous and subsequently release pollen, a variety of floral changes occur that discourage further insect visitation after pollination and allow the pollinators to escape on the second day of anthesis. On the first day of anthesis the flowers' strong carrion odor and color gradients draw pollinators toward the receptive gynostemium deep within the flower. Constricting floral tubes with trichomes oriented toward the gynostemium aid in capturing and holding the insects. On the next day, the flowers change to male phase and pollen is deposited on the pollinator. Flower structure and function then change to release the pollen-dusted pollinator. To aid in pollinator release, the floral odor disappears, color cues change, hairs relax, and the constricting areas of the tube are opened. Pollination appears to be a two-day process for any given flower with floral senescence by the third day. Floral visitors do oviposit in the flowers, but we suggest that this is not relevant to pollination. Comparisons are made with other Aristolochiaceae.

Key words: *Aristolochia grandiflora*, Aristolochiaceae, brood site provision, Calliphoridae, Diptera, insect interactions, Phoridae, pollination biology, protogyny, sapromyiophily, Staphylinidae.

There are many examples of how plants deceive their pollinators to ensure pollination events (Dafni, 1984; Proctor et al., 1996). In some of the more elaborate examples, the plant benefits from such interactions by securing the transport of its pollen, whereas the pollinator does not benefit. This is especially true for the Orchidaceae (containing the majority of species pollinated by deceit), as most insects will not eat pollinaria (Faegri & van der Pijl, 1979). However, in many examples of floral deceit some reward, including false pollen (e.g., Melastomataceae) and shelter (e.g., Araceae), are provided. Brood site mimicry, especially by scents and sometimes appearances of carrion, dung, and fungi, is well known in fly pollination through sapromyophily (Vogel, 1990; Larson et al., 2001) (or sapromyiophily of Proctor et al., 1996) and its equivalent involving beetles, saprocantharophily (Bernhardt, 2000). Although Faegri and van der Pijl (1979) combined the characteristics of both fly and beetle pollination by such deceit under the syndrome of sapromyiophily, characteristics of this syndrome include: more or less radial floral parts with depth; lantern-shaped floral parts with filiform appendages; dull floral colors (dark brown/purple/green) often checkered with dark spots; odor resembling that of decaying protein; the presence of osmophores (scent glands); the absence of nectar guides, nectar, or other primary resources (Faegri & van der Pijl, 1979; Vogel, 1990; Proctor et al., 1996). These features can be found in flowers of Asclepiadaceae, Araceae, Orchidaceae, Aristolochiaceae, Sterculiaceae, Rafflesiaceae, Hydnoraceae, Taccaceae, and Burmanniaceae. Sapromyiophily can occur with or without some form of imprisonment (trap or semi-trap blossoms) of the insect by the flower (Proctor et al., 1996; Faegri & van der Pijl, 1979).

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The Aristolochiaceae comprise six genera: *Aristolochia* L., *Asarum* L., *Saruma* Oliv., *Euglypha* R. Chodat & E. Hassl., *Holostylis* Rchb., and *Thottea* Rottb. (Pfeifer, 1960; Gonzalez, 1994). All are pollinated by deceiving their pollinators (although some species may self-pollinate; Burke, 1890; Petch, 1924; Hou, 1983), and some may or may not trap their pollinator. For example, the genus *Asarum* secures pollination by deceit but without imprisonment, as in *A. caudatum* Lindl., which attracts mostly mycophilous Diptera. In this case the flies, during oviposition within the flower, acquire pollen, but the larvae perish (Vogel, 1978a, 1978b). A genus that imprisons its pollinators is *Aristolochia*, comprising most of the 450 species within the family (Pfeifer, 1960, 1970; Gonzalez, 1994). Like many trap and semi-trap blossoms, *Aristolochia* has protogynous flowers. During the female phase floral visitors, pollinators or otherwise, are trapped within the flower to facilitate pollen deposition on the stigma. After pollination, visitors remain trapped within the flower until pollen is shed over them during the male phase of anthesis. After pollen release, the flower opens to allow pollinators to escape and carry pollen to another flower in female phase (Proctor et al., 1996). Although the general mechanism of pollination in Aristolochiaceae is understood from studies on various species such as *A. bracteolata* Lam., *A. clematitis* L., *A. littoralis* D. Parodi, *A. pilosa* Kunth, *A. grandiflora* Sw., *A. labiata* Willd., *A. linderi* A. Berger, *A. cordifolia* Glaz., *A. sipho* L'Hér., *A. tricaudata* Lem., *A. fimbriata* Cham. & Schltdl., *A. macroura* Gomes, *A. glaucescens* Kunth, *A. goldieana* Hook. f., and *A. arborea* Linden (Sprengel, 1793; Hildebrand, 1867, 1870; Delpino, 1873; Müller, 1873, 1883; Cooke, 1882; Correns, 1891, 1892; Ule, 1898a, 1898b, 1898c, 1898d, 1899, 1900; Knuth, 1909; Kirchner, 1911; Cammerloher, 1923; Carr, 1924; Petch, 1924; Knoll, 1956; Brantjes, 1980; Faegri & van der Pijl, 1979; Hou, 1983; Hilje, 1984; Hime & Costa, 1985; Wolda & Sabrosky, 1986; Razzak et al., 1992; Hall & Brown, 1993; Proctor et al., 1996), detailed studies on the pollination biology are scarce (see Cammerloher, 1923; Hilje, 1984; Hall & Brown, 1993), and there are few comparative studies between species (Brantjes, 1980; Sakai, 2002b).

One of the more complex examples of sapromyiophily is found in *Aristolochia grandiflora* Swartz, which produces one of the largest flowers of the Neotropical flora, and the largest in the Aristolochiaceae (ca. 35 cm diam.) (Knuth, 1909; Gonzalez, 1994). There are only two studies that attempt to explore the pollination biology of this species. Cammerloher (1923) studied its floral mechanisms at the Botanic Gardens in Bogor, Java, and Hilje (1984) worked mostly on the phenology of a natural population in Costa Rica. Although Cammerloher (1923) studied cultivated plants outside the natural Neotropical range of *A. grandiflora*, both authors described the pollination system of *A. grandiflora* as consistent with the syndrome of sapromyiophily with long-term imprisonment of the pollinators. However, these studies contrast in the type of pollinators and insect visitors observed in two disparate populations, namely those native to Java and Costa Rica, respectively. Because neither study provides a detailed assessment of the insect interactions and floral phenology of *A. grandiflora*, and because there is only sparse information on *A. grandiflora* in its native range, the results of further detailed observations contribute greatly to our understanding of the pollination biology of this species.

The goal of our research is to describe the pollination biology of *Aristolochia grandiflora* growing in its native habitat from a garden in Los Tuxlas, Veracruz, Mexico. In this study we address the following objectives:

1. Determination of the mechanisms of sapromyiophily for long-term imprisonment in *A. grandiflora*.
2. Assessment of the diversity and visitation rates of floral visitors to flowers of *A. grandiflora*.
3. Determination of whether flowers of *A. grandiflora* provide brood sites for flower visitors.

Materials and Methods

This study took place 1 km from La Estación de Biología Tropical de los Tuxtlas, in the lowland coastal rain forest of Veracruz, southeastern Mexico (28 Apr.–9 May 1997). *Aristolochia grandiflora* is known to be native to the area and flowers throughout the year (Ibarra Manríquez & Sinaca Colín, 1987; Hilje, 1984) and was found growing as a woody liana among cultivated vegetation in an open habitat. Fifteen separate flowers of *A. grandiflora* were used to make observations on floral structure and insect interactions.

In order to describe the mechanisms of sapromyiophily for long-term imprisonment (Objective 1), floral structures important to the pollination process of this species were measured on one-, two-, and three-day-old flowers (N = 8). These include overall condition of the flower, sexual stage of the gynostemium, color of various floral structures, and the presence/absence of odor. Herbarium speci-

mens were made of floral dissections and deposited at the Herbarium of the Universidad Nacional Autónoma de México in Mexico City.

To address Objectives 2 and 3, insect interactions were observed across all 15 flowers prior to, during, and after anthesis. In order to observe insect visitation, insects were counted visiting, entering, and leaving flowers on the first and second day of anthesis. Eight flowers were covered with mesh bags to capture all insect visitors to the flower. Flowers were then cut after the first, second, and third day of anthesis based on insect interactions with the flowers (i.e., fly entry and release). Two flowers were bagged prior to anthesis as controls. For example, Day 1: Three flowers bagged and cut for dissection after one day of fly entry (end of the first day of anthesis); Day 2: Three flowers bagged after one day of fly entry and cut for dissection at the end of the second day of anthesis; Day 3: Two flowers bagged after one day of fly entry and cut for dissection at the end of the third day of anthesis.

Bagged flowers were then taken to the field station at Los Tuxtlas for longitudinal dissection, observation, preservation, and photography. To count and identify (1) the insects contained within the flower and (2) the insects released from the flower but trapped within the mesh bags, bagged flowers were fumigated in sealed plastic bags with ethyl acetate to kill all floral visitors. Upon floral dissection, all floral visitors trapped within the flowers or bags were collected and preserved in 70% ethanol. Insects were not examined microscopically for pollen, although visual observations were made. A sub-sample of each of the insect families was taken to the Entomological Collection of the Autonomous University of Yucatán in Mérida for identification.

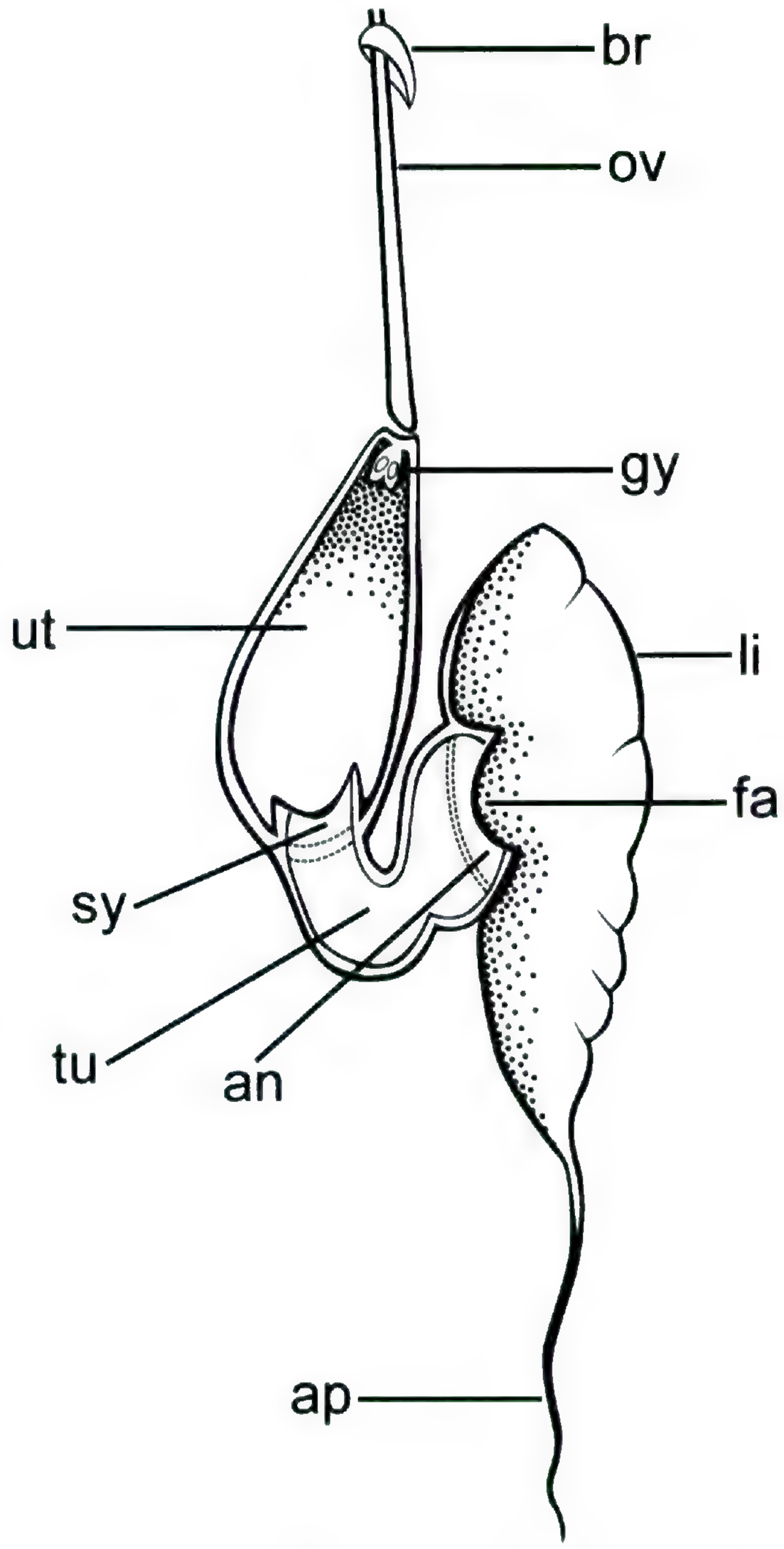

Figure 1. Morphological terminology of *Aristolochia grandiflora* floral structures: annulus (an), appendix (ap), bracteole (br), fauces (fa), gynostemium (gy), limb (li), ovary (ov), syrinx (sy), tube (tu), utricle (ut). (Re-drawn from Gonzalez, 1994.)

Observations and Results

Mechanisms of Sapromyiophily for Long-Term Imprisonment

Aristolochia grandiflora flowering patterns at our site are consistent with continual flowering systems of tropical lianas whereby relatively few flowers per plant are at anthesis at the same time (Hilje, 1984; Proctor et al., 1996). As in our study plants, such flowering patterns are indicative of limited self-pollination by geitonogamy. Flowers of *A. grandiflora* at our site also had functional and structural mechanisms consistent with those used to describe this species in the literature (Cammerloher, 1923; Hilje, 1984; Pfeifer, 1966). The flower (Fig. 1) has a uniseriate perianth, which includes a long filiform appendix (ap); the main perianth or limb (li); the fauces (fa) or opening of the flower; the entrance or annulus (an); a trichome-lined tube (tu) connected to the syrinx (sy), which opens into the inner chamber of the flower, the utricle (ut); male and female organs are located at the top of the utricle collectively called a gynostemium (gy); and the inferior ovary (ov) is subtended by a bracteole (br). General observations on floral odor revealed that *A. grandiflora* flowers one day prior to and during the first day of anthesis had a strong carrion scent, which disappeared by the second day.

Additional changes in overall floral form occurred during anthesis. As seen in Figure 2, the length measurements made between the utricle and the tube increased as the flower switched from fe-

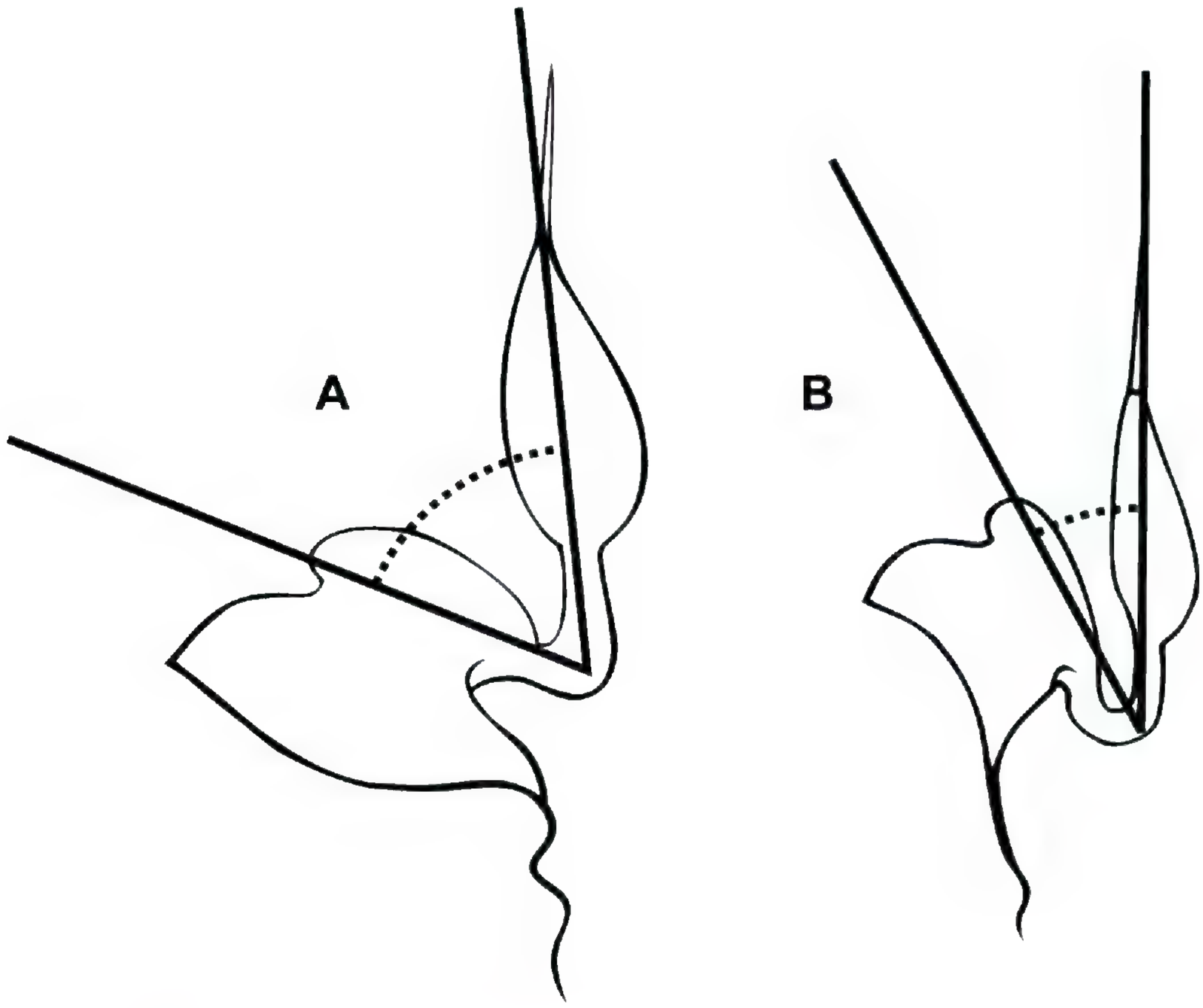

Figure 2. Relaxation of *Aristolochia grandiflora* floral structure to allow for insect departure on the second day of anthesis. —A. The angle between these floral structures increased to 60 degrees on the second day of anthesis. —B. The angle between the floral tube and utricle wall prior to pollination on the first day of anthesis is approximately 28 degrees.

male to male phase (an increase in angle from 28 to 60 degrees). Table 1 details changes in floral form, structure, and color over the first three days of anthesis. Observations are based on floral dissections made on one-, two-, and three-day-old flowers. The first day of anthesis, starting shortly after dawn, showed vibrant coloration of all structural components as the female phase of the gynostemium progressed. Most of the flower's structural components (annulus, tube, syrinx, and utricle) had erect trichomes and all had intact tissue. As the gynostemium switched from female to male phase on day 2 of anthesis, a general deterioration of the structural components of the flower initiated. As seen in Table 1, the tissue of both the syrinx and the utricle started to degrade, and the trichomes of all structures flattened. The limb also began to deteriorate and fold in at this stage, and discoloration of various structures started. By the third day of anthesis, the limb completely folded in, trichomes were mostly absent from all floral structures, and the tissues of all structures had started to decay and brown.

INSECT INTERACTIONS (VISITATION AND BROOD SITE PROVISION)

General observations of floral visitors to five *Aristolochia grandiflora* flowers revealed that on the day prior to the opening of the limb on the first day of anthesis, large (ca. 5 mm) Diptera (Calliphoridae) were observed congregating along the limb edge and on the appendix. Shortly after dawn on the first day of anthesis the carrion-like odor increased in intensity. Insect visitation was observed to peak between 9:30 and 10:30 A.M. Approximately 200 insects were observed to be entering each flower during peak visitation with activity dwindling to 13 insects between 11:30 A.M. and 12:00 noon. Even though visitation (the total number of insects entering a flower) dropped dramatically by noon, flowers remained open until the next day, potentially receiving more visitors, although this was not observed. A more detailed observation of floral visitation on the first day of anthesis showed that of those insects immediately identifiable to the researchers in the field, Coleoptera (ca. 7 mm) and small (ca. 2 mm) Diptera (Phoridae) were the primary visitors in the early morning, whereas large (ca. 5 mm) Diptera (Calliphoridae, Sepsidae, Muscidae, and Heleomyzidae) were only found to visit mid-morning, although Phoridae visitation continued throughout (Fig. 3).

Upon dissection of the flowers at the end of the first day of anthesis the average number of insects per flower was 454 (Table 2). Although most insects were Diptera: Phoridae (269) (ca. 2 mm) and Co-

Table 1. Floral structures important to the pollination process of *Aristolochia grandiflora* measured on eight flowers at the end of the first, second, and third day of anthesis. Measurements include overall status of the structure, status of trichomes on the structure (+ = erect; − = flattened), and notes on structure color (B = beige; Bl = black; Br = brown; P = purple; W = white).

Floral structure	Day 1	Day 2	Day 3
Limb			
Status	rigid and open	folding on guidelines	folded/decaying
Trichomes erect/flattened	absent	absent	absent
Color	checkered (P/W)	checkered (P/W)	P/Br
Annulus			
Status	rigid	soft	decaying
Trichomes erect/flattened	+	−	−
Color	P/Bl	P/W	P/Br
Tube			
Status	rigid	soft	decaying
Trichomes erect/flattened	+	+/−	−
Color	P to W	P to Br/W	Br
Syrinx			
Status	rigid	decay starting	decaying
Trichomes erect/flattened	+	−	−
Color	W	Br	Br
Utricle			
Status	rigid	decay starting	decaying
Trichomes erect/flattened	+	−	−
Color	spotted (W/P)	Br	Br
Gynostemium			
Stigma lobes			
Status	stigma receptive	stigma not receptive	decaying
Color	B	Br	Br
Anther			
Status	anthers closed	anthers dehisced	decaying
Color	B	Br	Br

leoptera: Staphylinidae (144) (ca. 7 mm), a number of large (ca. 5 mm) Diptera were found within the flowers, namely; Calliphoridae (13), Sepsidae (7), Muscidae (16), and Heleomyzidae (4). No insects were found in the mesh bags outside the flower at the end of the first day of anthesis.

On the second day after anthesis, release of large (ca. 5 mm) flies (Calliphoridae, Sepsidae, Muscidae, and Heleomyzidae) by relaxed angle of the perianth tube and flattening of trichomes (Fig. 2; Table 1) occurred between 8:00 A.M. and 9:00 A.M. This was followed by the release of smaller (ca. 2 mm) flies (Phoridae). Large (ca. 5 mm) flies (Calliphoridae, Sepsidae, Muscidae, and Heleomyzidae) were observed to leave the flower with large clumps of pollen on their back. Upon dissection of the flowers at the end of the second day of anthesis most insect taxa initially found within the one-day-old flowers were now inside the mesh bags but absent from the flower interior. These included all adult Diptera (Calliphoridae (9), Muscidae (4), and Heleomyzidae (1), and most notably the Phoridae (366)) (Table 2). Probably most notable was the presence of large numbers of Staphylinidae still within an average flower (218) and the occurrence of approximately 1000 Phoridae larvae on the utricle wall.

Dissections of bagged flowers cut after the third day of anthesis revealed that almost all the insects that were in the flower at the second day of anthesis were now only found outside the flower within the mesh bags (Table 2). These included Phoridiae (29) and the Staphylinidae (203). There was also a large number of Phoridae larvae found within three-day-old flowers (approximately 400), although numbers decreased from two-day-old flowers by more than 50% (Table 2).

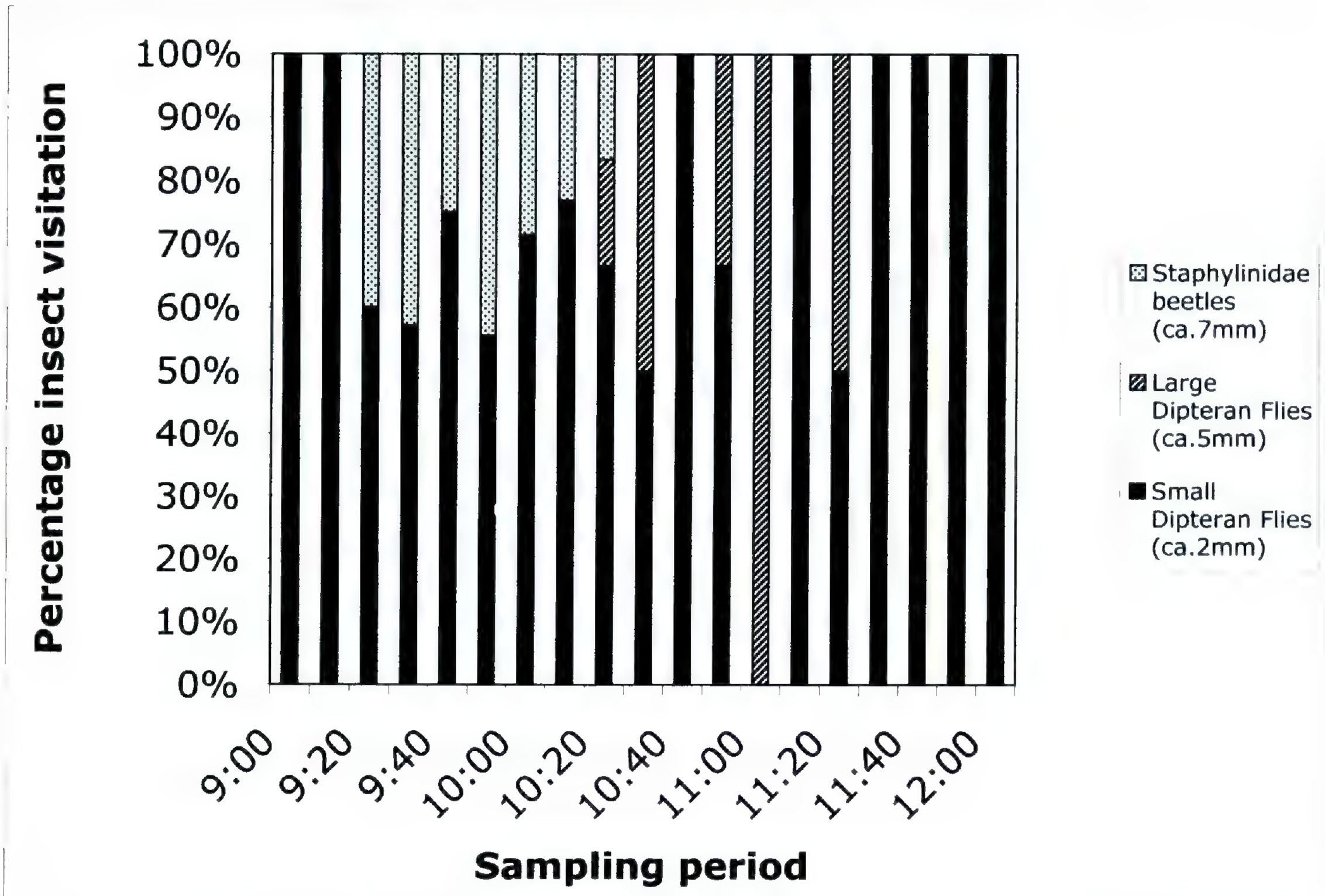

Figure 3. The average number of Dipteran flies (large and small) and *Staphylinid* beetles (Coleoptera) observed entering five flowers of *Aristolochia grandiflora* during peak visitation on the first day of anthesis. Means are expressed as a percentage of total insect visitation for each census period.

Discussion

Pollination and Mechanisms of Sapromyiophily for Long-Term Imprisonment

Although self-pollination has been suggested for some *Aristolochia* species (Burck, 1890, 1892a, 1892b, 1892c, 1894) our observations on *A. grandiflora* suggest that this is most unlikely. Our results indicate that pollination in *A. grandiflora* is consistent with the syndrome of sapromyiophily in odor, color, and floral structure (Table 1) and appears to be a two-day process. The protogynous flowers last only three days, but are attractive to pollinating insects (Diptera and Coleoptera) only on the first day of anthesis, which is when they are most odoriferous and in the pistillate phase, although a large number of insects are attracted by odor to the general vicinity of even the pre-anthesal flower. After pollination on the first day, anthers release pollen onto insects trapped within the utricle. On the second day of anthesis, pollen-laden insects escape after the flower goes through various changes in form and loses its scent. Mimetic color and floral structures appear to entice visitors into the depth of the perianth once odor has brought them to congregate in the general area (Faegri & van der Pijl, 1979; Dafni, 1984). Upon opening (Fig. 1), the large radial, funnel-shaped limb displayed a blotchy pattern of purple and white with blotchy purple guide-lines leading to the dark central cavity of the tube entrance or annulus (see Cammerloher, 1923; Hilje, 1984). Once the insect visitors have proceeded past the annulus, our observations from floral dissection suggest that insects are directed to the utricle (site of pollination) through a combination of floral structure (shape of tube and trichome orientation) and color changes (Table 1). The floral tube has grades in color from a dark purple near the annulus to the brighter, translucent utricle. Presumably, flies phototactically orient themselves to the light color of the utricle as suggested by Hilje (1984) and Cammerloher (1923). Within the flower there are two sites (Fig. 1) that act as filters for insect size selection (see Hilje, 1984; Brantjes, 1980). Between the perianth tube and the limb (annulus), and between the tube and the utricle (syrinx) are constricted areas covered with stiff trichomes pointing in toward the utricle that allow visitor movement in only one direction, as seems general for the genus (Knuth, 1909; Cammerloher, 1923; Hilje, 1984; Hall & Brown, 1993) (also see Table 1).

Table 2. Insects found inside the flowers or within mesh bags containing the flowers of *Aristolochia grandiflora*. Dissections were performed on eight flowers cut at: (1) the first day of anthesis (Day 1: three flowers bagged and cut after one full day of fly entry); (2) the end of the second day of anthesis (Day 2: three flowers bagged after one full day of fly entry and cut after fly release); and (3) the end of the third day of anthesis (Day 3: two flowers bagged after one full day of fly entry and cut one day after fly release). Taxonomic keys used were McAlpine et al. (1981–1987), Curran (1934), and Dear (1985).

			Day 1 dissection		Day 2 dissection		Day 3 dissection	
Order	Family	Genus	Average/ flower	Location found	Average/ flower	Location found	Average/ flower	Location found
Diptera	Calliphoridae	*Cochiomyia*	13	flower	9	bag	2	bag
		Chloroprocta						
Diptera	Sepsidae	*Nemopoda*	7	flower	0	—	0	—
Diptera	Muscidae	—	16	flower	4	bag	0	—
Diptera	Heleomyzidae	*Cinderella*	4	flower	1	bag	0	—
Diptera	Phoridae	*Spinophora*	269	flower	366	bag	29	bag
		Pericyclocera					4	flower
		Diplonerva						
		Dorniphora						
Diptera	Empididae	*Boreodronia*	1	flower	0	—	0	—
Hymenoptera	Formicidae	—	0	—	0	—	59	bag
Coleoptera	Staphylinidae	—	144	flower	218	flower	203	bag
							4	flower
Coleoptera	Nitintulidae	—	0	flower	1	bag	0	—
Homoptera	Cicadellidae	—	0	flower	1	bag	0	—
Diptera	Phoridae Larvae	—	0	flower	916	flower	396	flower
Total (excluding larvae)		—	454	flower	218	flower	8	flower
					382	bag	293	bag

The transition from pistillate to staminate phase is indicated by changes in floral odor, color, and structure (Table 1). The switch is reported to be physiologically triggered by the direct deposition of pollen onto the stigmatic surface of pistillate flowers (Pfeifer, 1966). Although limited to two flowers, our bagged controls to which insects had no access and thus pollen cannot have been deposited on the stigmas, showed changes as in open-pollinated flowers. We noted that in the staminate phase the overall structure of the flower appears to relax at the beginning of the second day of anthesis (Table 1; Fig. 2). The tube is no longer appressed to the utricle as the angle increases between these two floral structures. Hilje (1984) also noted an increase in the diameter of the restriction between the utricle and the tube at this stage in *Aristolochia grandiflora* (Fig. 1). Presumably this relaxation of the flower allows escape of the entrapped insects, now bearing newly deposited pollen loads from the dehiscence of anthers as observed in this study on the morning of the second day of anthesis. Contributing to the release of insects were changes in the trichomes (Table 1) throughout the tube and utricle that become either flattened or brittle, and lose unidirectional orientation (also noted by Knuth, 1909; Pfeifer, 1966) (Table 1). At the same time, probably contributing to insect release is the darkening of the utricle from translucent white of the first day of anthesis to brown in the second, which would reduce phototactic orientation (Table 1).

By the third day of anthesis the flower decays rapidly (Table 1). In general, floral senescence occurs and the calyx is either autodigested or falls (Knuth, 1909; Pfeifer, 1966). We did not observe persistent calyxes on fruits present at our site, although fallen flowers had withered and dried quickly (within two days: casual observations) in the sun.

The suite of characters (morphological, odor, and phenological) we describe occurs with sapromyiophily and allows for precise timing of events associated with successful pollination. The process depends on the long-term (ca. 1 day) imprisonment of the insect visitors. The exact timing of entry and exit of visitors to any *Aristolochia* species has not been recorded hitherto, but our observations showed a peak entry of insects around 10:00 A.M. on the first day of anthesis, and exiting around 8:30 the next morning.

INSECT INTERACTIONS (FLORAL VISITATION AND POTENTIAL POLLINATORS)

According to Brantjes (1980) some *Aristolochia* species are specialized to capture specific fly species or sizes, whereas many others capture a wide variety of organisms that may not be effective pollinators. Thus, the potential pollinators of any *Aristolochia* species are selected by floral size (as suggested by the review in Knuth, 1909) and the nature of the trap mechanism. Therefore, by measuring the visitor's thorax height and the distance between floral structures that act as filters, nonpollinators may be distinguished from potential pollinators (Brantjes, 1980). Petch (1924) conducted studies on the native small-flowered species *A. indica* L. and *A. bracteata* Retz in Sri Lanka and found that both were visited by a single insect species of *Ceratopogon* (Diptera: Ceratopogonidae). However, we demonstrated a wide range of Diptera, Coleoptera, Homoptera, and Hymenoptera imprisoned in the utricle of *A. grandiflora* (Table 2).

Our study agrees with previous studies on the pollination biology of *Aristolochia* that Diptera, especially Phoridae, Muscidae, and Calliphoridae, are the predominant pollinators (Table 2). Although high numbers of Staphylinidae were present in our flower dissections, there is no evidence for beetle pollination in our study. Bernhardt (2000) would interpret *A. grandiflora* as a generalist system incorporating both beetles and flies given that the species belongs to a genus of basal angiosperms. Because our study does not exceed the third day of anthesis, it is plausible that beetles may yet emerge with viable pollen from rotting flowers. However, studies consistently report that pollen is carried on the backs of Dipteran thoraces (Delpino, 1873; Knuth, 1909; Hilje, 1984; Brantjes, 1980; Hall & Brown, 1993), indicating that the flies walk on the utricle wall and have pollen deposited from the gynostemium (Correns, 1891; Knuth, 1909). We found most fly visitors to *A. grandiflora* were small Phoridae, but based on our visual observations large Calliphoridae and Muscidae were the flies that carried pollen (Table 2). Although Phoridae visitation was high, we suggest that the Phoridae are not effective pollinators for this species. Hilje (1984) also found that the most abundant visitors to *A. grandiflora* flowers were Phoridae, but noted that it was unlikely they were the pollinators because they carried relatively little pollen. He, too, indicated instead larger flies of the families Otitidae and Muscidae. In Java, Cammerloher (1923) indicated that the pollinators of *A. grandiflora* were large Calliphoridae even though he found the principal visitors to be smaller Anthomyidae. The specific difference between our results and the two previous studies may reflect differences in geographic location, time of year, the availability and diversity of pollinators, or combinations thereof. Cammerloher

(1923) studies were conducted outside the native habitat of *A. grandiflora*, and Hilje (1984) did not document floral changes and phenology to the level of detail that we provide.

INSECT INTERACTIONS (PROVISION OF REWARDS: BROOD SITES, MATES, FOOD, PREY)

We found a large community of Phoridae larvae living on the utricle wall of flowers of *Aristolochia grandiflora* indicating oviposition by visiting insects (Table 2). Little is known about provision of brood sites within the Aristolochiaceae. *Asarum caudatum* provides a site for oviposition, but larvae die (Proctor et al., 1996). Some investigators of *Aristolochia*, including those studying *A. grandiflora*, who found larvae of Phoridae, Muscidae, and Drosophilidae within the flowers have shown that the utricle wall acts as a brood site (Hall & Brown, 1993; Hilje, 1984), but again without larval survival. Wolda and Sabrosky (1986) studied flies associated with the flowers of *A. pilosa* in Panama and found no evidence of oviposition. They also noted that no males were ever reported inside the flowers. Three studies of different *Aristolochia* species in Panama have shown female-biased trapping (Wolda & Sabrosky, 1986; Carr, 1924; Hime & Costa, 1985), but for *A. littoralis* in Florida, the bias is mainly to males, presumably attracted by a female sex pheromone mimic (Hall & Brown, 1993). For *A. grandiflora*, insect visitors of both sexes have been shown (Cammerloher, 1923; Hilje, 1984), indicating that co-habitational sequestration may promote mating.

It has been suggested that some *Aristolochia* species may provide food rewards to visitors (Knuth, 1909); these include nectar, e.g., *A. clematitis*, and mucilaginous stigmatic exudates (Hilje, 1984; Wolda & Sabrosky, 1986) although nectaries were not found in our study species. Whether or not there is a benefit for the pollinator for its services to the plant is incompletely known, and rewards may vary from species to species of *Aristolochia* and pollinator. Within the utricle lives a diverse community of Coleoptera, Diptera, and Hymenoptera that may show interesting predator/prey interactions (Hilje, 1984) (Table 2). The flower attracts many predators to the utricle, possibly in search of protein-rich larvae (Hilje, 1984). The primary predators for both Hilje (1984) and our study were Staphylinidae (Coleoptera). The fact that Staphylinidae did not escape from *A. grandiflora* flowers until the third day of anthesis (Table 2) suggests that they may obtain some benefit, possibly prey, from remaining Phoridae larvae. A greater than 50% decrease in larval counts within day 3 flowers as compared to that of day 2 also suggests the possibility of predation by Staphylinidae (Table 2). However, in *A. grandiflora* Petch (1924) suggested that a toxic chemical stored in the utricle wall protects developing maggots from predation.

CONCLUSIONS

Aristolochia grandiflora is a short-lived flower (3 days) of a continual blooming tropical liana. Its suite of characters, including form and color of the perianth, odor (its production and cessation thereof), floral movements (including trichomes and the perianth as a whole) with aging, and definitive protogyny, place the flower within the syndrome of sapromyiophilous trap blossoms (Faegri & van der Pijl, 1979). We suggest that the most effective pollinators are the large (ca. 5 mm) Diptera (Calliphoridae, Muscidae, Sepsidae, Heleomyzidae). Although we did not quantify our observations, they were seen exiting our study flowers with visible dustings of pollen on their bodies. The flowers also attract and trap large numbers of small beetles (Staphylinidae) and small Diptera (Phoridae); however, we cannot assess the role of Phoridae and Staphylinidae as pollinators. Although brood site provision can attract pollinators to the flowers of some *Aristolochia* species (Disney & Sakai, 2001; Sakai, 2002a, 2002b), we cannot conclude this from our study. The large Diptera (Calliphoridae, Muscidae, Sepsidae) have larval developments that are typically more than a week (Smith, 1986), and much longer than the life of the flower, where the falling flowers of *A. grandiflora* in our study were withered and dried within two days. The small Diptera (Phoridae) may be able to mature on rotting flowers provided they remain moist for long enough (e.g., at least a week (Disney, 1983, 1989)). The flowers do not appear to provide nectar and we did not determine if the flies ingested pollen, but those families we found are not noted for pollenivory, except for possibly some Muscidae (Larson et al., 2001). Thus, we do not invoke mutualism between the flies and the flowers, but rather attraction by deceit (Dafni, 1984). Results from our floral dissections and observations indicate a reduction in Phoridae larvae in the presence of large numbers of Staphylinidae beetles. Based on our observations, it is possible that the beetles found within *A. grandiflora* flowers (e.g., Staphylinidae) may be predatory and feed on Dipteran eggs and larvae deposited in the flowers, but this idea remains to be tested.

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EXPERIMENTAL EVIDENCE OF POTENTIAL FOR PERSISTENT SEED BANK FORMATION AT A SUBANTARCTIC ALPINE SITE IN TIERRA DEL FUEGO, CHILE[1]

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Abstract

Seed burial experiments were conducted for 15 alpine species derived from 15 genera and 12 plant families from a subantarctic location on Cerro Riñón, Tierra del Fuego, 54°S, Chile. Batches of seed buried at 5 cm depth at 550 m elevation in February 1996 were exhumed after 335, 363, and 755 days, and their status and viability determined. Thirteen species (87%), one marginally (*Acaena magellanica, Anemone multifida, Azorella lycopodioides, Bolax gummifera, Calceolaria biflora, Caltha appendiculata, Draba magellanica, Empetrum rubrum, Gentianella magellanica, Gunnera magellanica, Luzula alopecurus, Oremomyrrhis hookeri* (marginal), *Pernettya pumila*), were judged as having potential to form a persistent soil seed bank, while two (*Senecio magellanicus, Berberis buxifolia*) only showed evidence of a transient seed bank. Seed viability in residual intact seeds was high and showed little tendency to diminish over the two-year experimental period, indicating optimal conditions for seed survival in the alpine soil. Fits of the number of remaining viable seeds at each exhumation date to the negative exponential model gave maximum seed longevity estimates of 1623 days in *Draba magellanica*, 2779 days in *Empetrum rubrum*, 3026 days in *Gunnera magellanica*, 777 days in *Oreomyrrhis hookeri*, and 5983 days in *Pernettya pumila*. Estimated seed longevities for some species at the subantarctic alpine site are among the highest reported for alpine species to date.

Key words: Chile, persistent seed bank, seed burial experiments, seed viability, Tierra del Fuego, transient seed bank.

Examination of soil cores for viable and/or germinable seeds has revealed the existence of extensive soil seed banks in arctic and alpine vegetation at several Northern Hemisphere locations (e.g., McGraw & Vavrek, 1989, and references therein; Ebersole, 1989; Hatt, 1991; Ingersoll & Wilson, 1993; Chambers, 1993, 1995; Diemer & Prock, 1993; Molau & Larsson, 2000). McGraw and Vavrek (1989) estimated that up to one half or more of the species present in the standing vegetation in alpine and arctic sites could be found in the seed bank.

Although the study of soil cores has been useful in ascertaining that sexual reproduction is a common feature in the cold and harsh alpine and arctic habitats, few studies have been carried out in such a way as to be able to distinguish clearly between the transient and persistent components of the soil seed bank (e.g., Roach, 1983; Ebersole, 1989; Ingersoll & Wilson, 1993). The soil core method has an additional disadvantage. Because soil cores contain seeds produced over a number of years, even with careful sampling so as to exclude seeds corresponding to the present year's seed rain, very little can be said about the longevity of seeds beyond one year. Longevity of seeds in the soil constitutes the vital information required for understanding the relevance of a persistent seed bank in the context of life-history theory (Brown & Venable, 1986; Rees, 1996), and for the successful restoration of degraded areas in many alpine and arctic sites (e.g., Urbanska, 1997).

An alternative approach is to experimentally bury batches of seeds of known age in the soil, retrieving and examining samples for viability and/or germinability at a series of programmed future

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dates (Baskin & Baskin, 1998). This method has been employed for single or small numbers of species from several habitats (e.g., grassland: Pavone & Reader, 1982; tropical: Lonsdale et al., 1988; sand dunes: Zhang & Maun, 1994) including high mountains (Guariguata & Azocar, 1988; Spence, 1990; Cavieres & Arroyo, 2001; Schwienbacher & Erschbamer, 2001). Nevertheless, the majority of these studies have been focused on single species. For example, Guariguata and Azocar (1988) buried seeds of the long-lived, dominant paramo species *Espeletia timotensis* Cuatrec. (Asteraceae) in its natural habitat for a period of one year. Spence (1990) performed a seed burial experiment of just over one year's duration on *Chionochloa macra* Zotov (Gramineae), dominant in the low alpine region in the Craigieburn Range in New Zealand. Cavieres and Arroyo (2001) performed a seed burial experiment of 3 years' duration with the perennial herb *Phacelia secunda* J. F. Gmel. at different elevations in the Andes of central Chile. Only Schwienbacher and Erschbamer (2001) have experimentally evaluated the persistence of seeds in the soil for nine species in the Austrian Alps at 2400 m a.s.l. However, they evaluated the fraction of seeds that remain viable in the soil only after eight months' burial, reporting that six species showed high percentages of seeds that remain ungerminated; in only three of those species was there certainty that the remaining ungerminated seeds were viable.

In this paper, we report the results of seed burial experiments of 2 years' duration carried out at a subantarctic alpine location in Tierra del Fuego (54°S), Chile, in order to detect the potential for persistent seed bank formation. Persistent seed banks, by definition (Thompson et al., 1998), are those in which a fraction of the seeds of a species not only remain in the soil, but are also viable for at least one year after production. First, we determine whether 15 alpine species individually exhibit potential to form a persistent seed bank. Second, we attempt to fit mathematical functions to our seed burial results in order to estimate the length of time seeds of the species studied could potentially remain viable in the soil. Third, we assessed whether the persistence of seeds in the soil is related with other characteristics of the seed such as the size and shape, as it has been shown in other ecosystems (e.g., Thompson et al., 1993).

Materials and Methods

Study site

Work was conducted in the alpine belt immediately above the *Nothofagus pumilio* (Poepp. & Endl.) Krasser tree line lying at 450–500 m elevation, on Cerro Riñón (54°S), located in the Patagonian Andean complex on the edge of the forest-steppe boundary in Tierra del Fuego (Fig. 1). As is found on inland mountains throughout Tierra del Fuego, the dominant species are cushion plants (*Bolax gummifera* (Lam.) Spreng. (Apiaceae), *Azorella lycopodioides* Gaud. (Apiaceae)) and the prostrate shrub *Empetrum rubrum* Vahl ex Willd. (Empetraceae), these being accompanied by many caespitose and rosette perennial herbs and slender grasses (Moore, 1983; Arroyo et al., 1996; Mark et al., 2001). Flowering in the eastern mountains of Tierra del Fuego occurs from close to snow melt in early October through to early March. Although not quantified, peak fruiting occurs in the interval of February to early March.

Available climatic data for the general area of Cerro Riñón are limited. Annual precipitation on the forest-steppe boundary, based on a climatic station at Cameron (53°40'S, 69°53'W), is 503 mm with more than 50% of precipitation falling in summer. In the windy, arid climate of inland Tierra del Fuego (based on field observations from 1995, 1996, and 1997), permanent snow was present above the tree line on Cerro Riñón every year for five months (May through September). Mean annual temperature at Pampa Guanaco (200 m a.s.l.) located some 19 km west of Cerro Riñón is 2.7°C, while mean monthly temperature during the late spring to late summer (October–April) is ca. 6.0°C.

Seed sources

Bulk seed collections were made on Cerro Riñón during March 1996. Species included perennial herbs, cushion species, shrubs, and one annual-biennial herb. The choice of species was made so as to maximize the taxonomic coverage of a manageable number of species, while at the same time representing a mixture of dominant and subdominant taxa. Mature seeds at the point of being dispersed or seeds recently dispersed around a mother plant were collected from some 30 or more individuals. When we collected seeds on the soil surface or lodged within the foliage of a mother plant, we made a special effort to distinguish between the current and earlier years' seeds. The field seed collections were carefully checked under a binocular microscope for the presence of any aborted and immature seeds, the latter being discarded. Adequate amounts of filled seed were amassed for 15 species (Table 1). For each species, 30 seeds were randomly selected and measured under the binocular microscope in order to obtain their lengths and

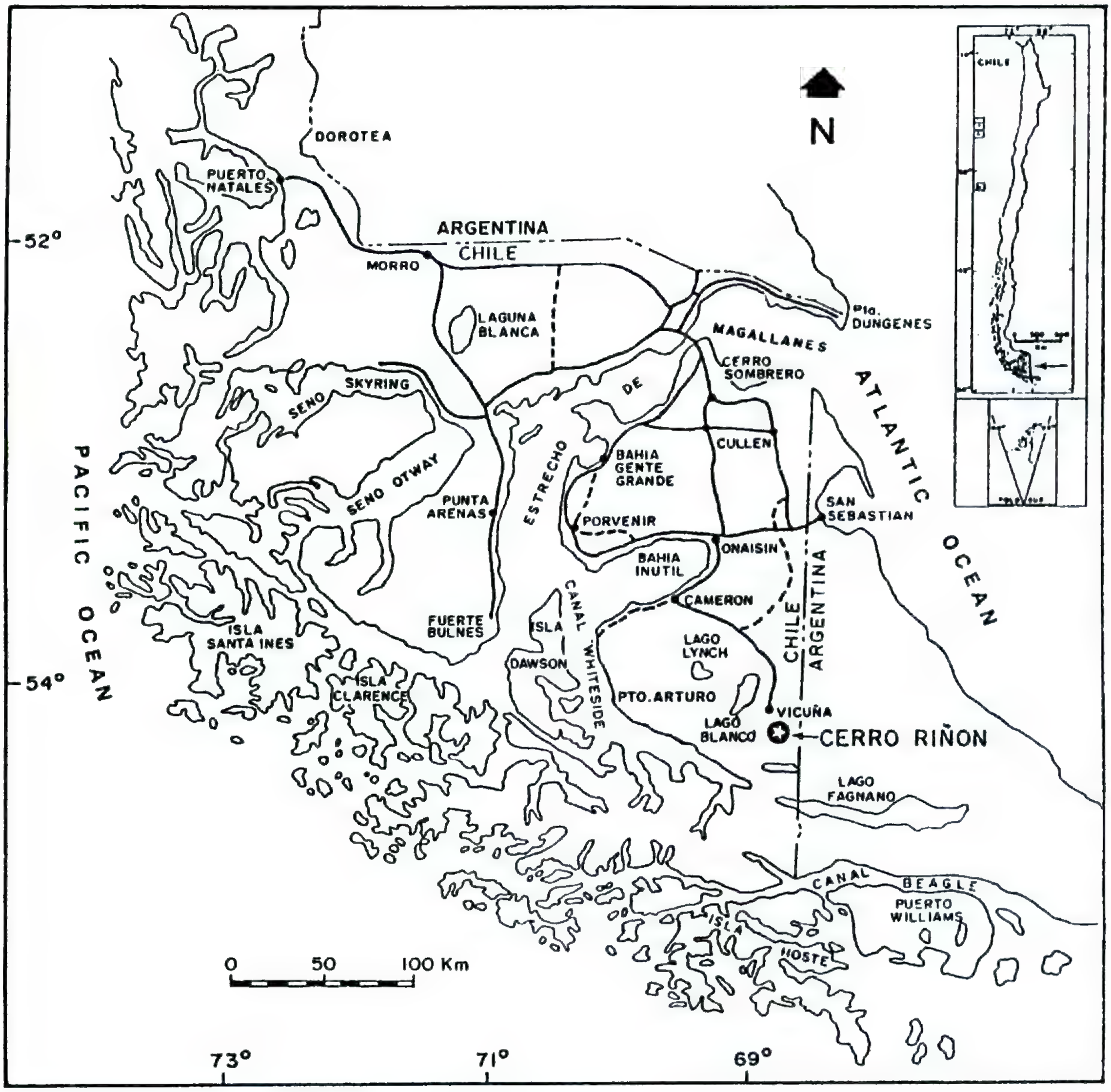

Figure 1. Location of Cerro Riñón in central Tierra del Fuego, Chile.

widths; after that seeds were weighed in a digital balance (OHAUS). In species with extremely small seeds (e.g., *Calceolaria biflora*), these were weighed in groups of 20 seeds each.

Within 1 to 2 days of collection in the field, 50 seeds of each species were subjected to the Tetrazolium chloride test (Moore, 1973) in order to assess their initial viability.

Over the period 12–14 March 1996 three sets of six batches per species of 30–39 seeds (total of 18 batches per species) were counted out and introduced into 10 × 10 cm nylon mesh envelopes of three sizes, electing a smaller mesh size than the introduced seeds. The envelopes containing the seeds for each of the 15 species were separated into three sets, each of six replicates. For every set of species in a given replicate, the species was assigned a number between 1 and 15 randomly, for later positioning in the buried seed cages.

SEED BURIAL

On 15 March 1996 seeds were transported back to the field to a burial location on a southeast-facing slope at 550 m, where six randomly placed replicate burial sites within an area of approximately 50 × 50 m were previously established. The general burial area, which was flatter than the surrounding slopes on average, was dominated by *Bolax gummifera* and *Azorella lycopodioides* with some lichen and moss growth at the soil surface, good soil development, and moderate drainage. At each of the

Table 1. Life-form and seed characteristics of the species studied in assessment of potential persistent seed bank formation in the alpine zone on Cerro Riñón, Tierra del Fuego. A-B = annual to biennial herb; PH = perennial herb; CU = cushion-forming perennial herb; SH = shrub.

Species	Family	Life-form	Weight (mg)	Length (mm)	Width (mm)	Seed shape
Acaena ovalifolia Ruiz & Pav.	Rosaceae	PH	1.49	3.7	1.7	cupule obconical
Anemone multifida Poir.	Ranunculaceae	PH	1.34	4.0	2.0	achene asymmetrically ovate
Azorella lycopodioides Gaud.	Apiaceae	CU	0.60	1.7	2.0	ovoid
Berberis buxifolia Lam.	Berberidaceae	SH	6.33	5.0	2.0	lunate, smooth
Bolax gummifera (Lam.) Spreng.	Apiaceae	CU	1.29	3.0	2.0	ovoid
Calceolaria biflora Lam.	Scrophulariaceae	PH	0.03	0.7	0.3	navicular, reticulate
Caltha appendiculata Pers.	Ranunculaceae	PH	0.33	1.7	0.9	ovoid, ellipsoid
Draba magellanica Lam.	Cruciferae	PH	0.15	1.0	0.8	ovoid, smooth
Empetrum rubrum Vahl ex Willd.	Empetraceae	SH	0.25	1.8	1.2	ovoid
Gentianella magellanica (Gaud.) Fabris ex D. M. Moore	Gentianaceae	A-B	0.15	0.8	0.5	ovoid
Gunnera magellanica Lam.	Gunneraceae	PH				ovoid
Luzula alopercurus A. N. Desv.	Juncaceae	PH	0.25	1.3	0.7	cylindrical
Oreomyrrhis hookeri Mathias & Const.	Apiaceae	PH	0.87	3.5	1.5	oblong
Pernettya pumila (L.f.) Hook.	Eriacaceae	SH	0.11	1.0	0.7	ovoid
Senecio magellanicus Hook. & Arn.	Asteraceae	PH	1.35	4.0	2.0	achene cylindrical

six replicate sites, three rectangular areas separated by 5–10 cm of untouched turf were excavated to allow for the introduction of three wire cages (70 cm long × 40 cm wide × 5 cm tall). A layer of sieved soil was placed in the open cages after they had been introduced into the burial sites. One envelope of seeds per each of the 15 species was placed over the sieved soil, respecting the previously established randomized order. The seed envelopes were covered with additional sieved soil, and the cages carefully adjusted in the ground such that the envelopes lay 5 cm below the soil surface. Roach (1983) found that the great majority of the seeds fail to penetrate further than 5 cm depth in soil of arctic and alpine sites. The cages were wired closed and covered with additional sieved soil and the original excavated turf, which had been carved thinner so as to lie at the level of the surrounding vegetation. The wire cages served to prevent any downslope movement of the seed envelopes and as deterrents for the small burrowing mammal *Cieno-mys magellanicus*, which has been observed by us to occur above tree line on nearby mountains in Tierra del Fuego. The position of each replicate burial site was marked, and the three cages per each of the six burial sites identified as to number. We randomly assigned positions 1–3 to each of the three cages at each of the six sites for later exhumation on three separate dates.

RETRIEVAL OF BURIED SEEDS

In accordance with the previously randomized order for retrieval, at each replicate site a set of six cages was exhumed on the following dates: (1) 14 February 1997; (2) 14 March 1997; (3) 10 April 1998. The first exhumation date was planned so as to be fairly sure that any current year's seed germination taking place after the winter period would have already occurred. The second date was planned toward the end of the summer–autumn season so as to assess the viability of any remaining seeds after one year's burial and to assess any late summer seed mortality. The third date was planned so as to allow the seeds to remain in the soil for at least 2 full calendar years, thus allowing us to judge the potential for the formation of a persistent seed bank. Remaining intact ungerminated seeds retrieved on each of the exhumation dates were subjected to the Tetrazolium chloride test, using the same protocol as outlined earlier so as to determine the seed viability.

DATA ANALYSIS

The recovered intact seeds demonstrated as viable on the basis of the Tetrazolium test, expressed

as a percentage of initial buried seed number, provided a measure of the "potential" persistent seed bank (Zhang & Maun, 1994). To assess loss of total viable seeds over time (and hence depletion of the potential soil seed bank) and estimate maximum seed ages, we used the negative exponential model (Guariguata & Azocar, 1988; Lonsdale et al., 1988), linearized for statistical application: $\ln N_t = \ln N_0 - kt$, where N_t = mean number of viable seeds at time t days; N_0 = mean initial number of viable seeds. The accepted significant level for the linear regressions was $P < 0.05$. The age of the last viable seed for a species was determined by the equation $t = \ln N_0/k$.

Relationships between seed persistence and seed size and shape were assessed through linear regressions between the percentage of ungerminated seeds after 2 years' burial (arcsin transformed for normalization) with the seed weight (log transformed) and the quotient width/length as suggested in Schwienbacher and Erschbamer (2001).

Results

Seeds of most of the study species were very small. Seed size ranged from 1.3 mg weight, 4 mm long, and 2 mm wide in *Senecio magellanicus*, to 0.03 mg, 0.7 mm long, and 0.3 mm wide in *Calceolaria biflora* (Table 1). The most common seed shape was ovoid, followed by cylindrical achene (Table 1).

The percentage of viable seeds in relation to initial buried seed number (Table 2) reveals a wide range of situations among the 15 species studied after being buried 2 years. By the end of the 2-year period, not a single seed of *Acaena ovalifolia, Calceolaria biflora, Caltha appendiculata, Luzula alopecurus,* or *Azorella lycopodioides* had germinated or decayed. For these same species, terminal seed viability as deduced from the Tetrazolium chloride test was over 80%, and indeed close to 100% in a number of cases (Table 2). Similar, but less rigid, behavior was seen in *Anemone multifida* and *Gentianella magellanica,* where a small percentage of the buried seeds had either germinated or were decayed, with again a very high percentage of the remaining ungerminated seed fraction remaining viable (Table 2). For a third group of species, composed of *Gunnera magellanica* and *Pernettya pumila,* around half of the seeds had germinated after the 2-year burial period. However, remaining seeds continued to exhibit high viability. In three species (*Bolax gummifera, Draba magellanica,* and *Empetrum rubrum)* around ⅔ to ¾ of the seeds had exited the seed bank through germination or other causes

Table 2. Status of exhumed seeds (mean ± SE) in the alpine zone on Cerro Riñón 335, 363, and 755 days after burial date. N = 6 replicates.

Species	Buried 335 days		Buried 363 days		Buried 755 days	
	Ungerminated (% intact seeds)	Viable seeds (as % of intact seeds)	Ungerminated (% intact seeds)	Viable seeds (as % of intact seeds)	Ungerminated (% intact seeds)	Viable seeds (as % of intact seeds)
Acaena ovalifolia	100 ± 0	98.9 ± 1.0	100 ± 0	78.3 ± 6.6	100 ± 0	87.8 ± 3.4
Anemone multifida	100 ± 0	90.6 ± 5.9	96.7 ± 1.4	77.2 ± 5.9	95.8 ± 3.8	95.8 ± 3.8
Azorella lycopodioides	100 ± 0	78.5 ± 13.2	100 ± 0	74.7 ± 5.9	81.2 ± 2.8	81.2 ± 2.8
Berberis buxifolia	10.0 ± 7.5	83.3 ± 6.8	0 ± 0	—	—	—
Bolax gummifera	100 ± 0	95.4 ± 2.0	56.0 ± 12.1	81.9 ± 8.7	57.6 ± 11.9	57.6 ± 11.9
Calceolaria biflora	100.0 ± 0	79.6 ± 6.7	100 ± 0	81.7 ± 5.9	98.9 ± 0.6	98.9 ± 0.6
Caltha appendiculata	100 ± 0	82.3 ± 6.0	98.9 ± 1.0	9.1 ± 4.5	96.8 ± 1.3	96.8 ± 1.3
Draba magellanica	60.2 ± 12.9	100 ± 0	44.6 ± 4.7	98.6 ± 1.3	57.8 ± 12.9	57.8 ± 12.9
Empetrum rubrum	74.4 ± 11.1	95.1 ± 2.9	85.0 ± 4.7	94.0 ± 2.5	98.7 ± 1.2	98.7 ± 1.2
Gentianella magellanica	93.9 ± 3.1	53.2 ± 7.2	88.2 ± 2.1	57.1 ± 8.3	94.3 ± 2.6	94.3 ± 2.6
Gunnera magellanica	100 ± 0	76.5 ± 8.3	93.6 ± 5.9	77.8 ± 8.5	78.5 ± 9.0	78.5 ± 9.0
Luzula alopercurus	100 ± 0	100 ± 0	50.9 ± 8.3	45.0 ± 9.4	98.9 ± 1.0	98.9 ± 1.0
Oreomyrrhis hookeri	32.8 ± 5.7	73.8 ± 6.6	25.3 ± 3.6	98.2 ± 1.7	—	—
Pernettya pumila	92.7 ± 6.7	96.4 ± 1.2	100 ± 0	77.8 ± 8.5	93.7 ± 3.1	93.7 ± 3.1
Senecio magellanicus	15.4 ± 5.8	53.7 ± 16.3	0 ± 0	—	—	—

Table 3. Potential to form a persistent seed bank in the subantarctic alpine zone, Tierra del Fuego, 54°S, as adduced from seed burial experiments. Species are arranged according to their potential to form a persistent seed bank versus a transient seed bank. Species showing short persistent seed banks.

Long	Short	Transient seed banks ⇒		⇐ Persistent seed banks
Acaena ovalifolia	*Bolax gummifera*	*Oreomyrrhis hookeri*	*Berberis buxifolia*	*Anemone multifida*
Calceolaria biflora	*Draba magellanica*		*Senecio magellanicus*	*Gentianella magellanica*
Caltha appendiculata	*Empetrum rubrum*			
Luzula alopecurus				
Azorella lycopodioides				

Table 4. Significant adjustment ($P < 0.05$) to the negative exponential model for loss of viable seed with time in species from subantarctic alpine zone in Tierra del Fuego, 54°S.

Species	R^2	Predicted maximum seed longevity (days)
Draba magellanica	0.874	1623
Empetrum rubrum	0.881	2779
Gunnera magellanica	0.932	3026
Oreomyrrhis hookeri	0.923	777
Pernettya pumila	0.890	5983

within 2 years, with less than ⅓ of the original seed number remaining viable. In the remaining species (*Oreomyrrhis hookeri*, *Berberis buxifolia*, and *Senecio magellanicus*) no seeds remained intact and viable after 2 years. In *O. hookeri*, although a fraction of the seed (25%) had not germinated and remained highly viable at the end of the first summer season, none remained in this state by the end of the second autumn. In *Berberis buxifolia* and *Senecio magellanicus* practically all seeds had germinated or had decayed by late summer the first year, and all had germinated or decayed by the time a full calendar year had expired. Summarizing these results (Table 3), 13 species (87%) on the subarctic alpine site showed some potential to form a persistent seed bank, with seven showing no decay on seed viability after 2 years' burial.

Table 4 shows the species with viable seeds after 2 years' burial in which there was a statistically significant fit for number of viable seeds over time with the negative exponential models. We only obtained significant fits for five species, where estimates of the longevity of seeds buried for these species revealed a range from 16.4 years (*Pernettya pumila*) to 4.2 years (*Draba magellanica*). We failed to obtain significant fits in other species because percent viability in residual physically intact seeds among the three exhumation dates showed that there were statistically higher terminal viability (755 days' burial) in relation to seeds exhumed in early autumn the previous year (363 days' burial). This was the case of *Gentianella magellanica*, *Anemone multifida*, *Caltha appendiculata*, and *Luzula alopecurus*. Such a result could accrue if physically less apt (more prone to loss of viability) seeds were more abundant among the intact seeds at the time of the earlier exhumation date and had been progressively weeded out with time. However, the percentage of seeds in the germinated and decayed category stayed relatively constant in these same species over time, such that there was little change

in the proportion of intact seeds over the 2-year period (Table 2). One-Way ANOVA performed with arcsin transformed for percentage of seed remaining intact showed no significant differences in *A. multifida* (F = 1.663, NS), *C. appendiculata* (F = 1.000, NS), and *G. magellanica* (F = 2.411, NS) throughout the length of the experiment. A similar result was obtained in *O. hookeri* (t = 0.9204, NS). The percentage of intact seeds in *L. alopecurus* remained at 100% over the entire experimental period (Table 2).

Linear regresssions showed that neither seed size nor seed shape were significantly related with the percentage of seeds that remained ungerminated after 2-year burial. That is, among the studied species, independent of the seed size and shape, a high percentage of seeds remained ungerminated in the soil after 2 years' burial.

Discussion

As far as we are aware, our study would appear to constitute the first experimental seed burial study for an alpine habitat in which a taxonomically diverse set of species (representing 15 genera and 12 families) has been studied simultaneously and under identical conditions for more than one year. Including the marginally persistent seed bank species, *Oreomyrrhis hookeri*, we have found that 87% of the species studied showed potential to form a persistent seed bank because they maintained an important fraction of viable ungerminated seed after 2 years' burial. If we consider that the total number of species just above tree line in the alpine region of Tierra del Fuego is ca. 25–30 species (Mark et al., 2001), according to our results at least 50% have the potential to form a persistent seed bank. Thus, considering the definition of persistent seed bank, our results suggest a fairly generalized potential for persistent seed bank formation in the subantarctic alpine habitat, with significant seed longevity in a number of species.

Results obtained for alpine and arctic habitats with the use of the soil core method have found a variety of results in terms of percentage of species present in the persistent component of the seed banks. For instance, Roach (1983) found 5 out of 6, and 13 out of 35 species represented in the standing vegetation to be present in the persistent seed bank at two tundra sites in the Brooks Range, 790 m in Alaska (68°20'N). Ebersole (1989) studied four tundra communities at Oumalik (69°N) on the edge of Alaska's Arctic Coastal Plain, and registered persistent seed banks for 37–58% of the species in the surrounding vegetation. Ingersoll and Wilson (1993) studied a treeless high subalpine site on Mount Jefferson (44°45'N) in Oregon, reporting a persistent seed bank comprised of 12 (55%) of the 22 standing vegetation species. Arroyo et al. (1999) detected persistent soil seeds representing 31% of the species in the standing vegetation at a high alpine site (3250 m) in the central Chilean Andes.

Percentages of persistent seed bank species obtained with the soil core method are generally lower than found in the present experimental study. The fewer persistent seed bank species detected in general surveys with the soil core method may partially be a result of a high probability of missing rare species in the persistent seed bank. It should also be borne in mind that in our study, burying seeds 5 cm beneath the soil surface might be somewhat artificial in terms of light penetrance, nutrients, and drainage. Roach (1983) found a striking reduction in seedling emergence comparing the second and first 5-cm layers of soil in Alaskan tundra, suggesting that the great majority of the seeds fail to penetrate further than 5 cm. As Chambers et al. (1991) pointed out, however, seed entrapment in alpine areas is highly dependent upon such factors as particle size, soil porosity, and seed size itself. In general, substrates in the South American Andes are strongly porous with much coarse material found at the surface as a result of wind erosion, which, added to the small size of seeds found in this study, could favor the formation of persistent seed bank in this habitat.

Exclusion of predators in our experimental burials could also be an additional contributory factor for the difference, although no evidence of burrowing animals was seen at the particular site. By excluding large seed predators, we have possibly overestimated real species richness in relation to the local persistent soil seed bank.

While alpine seeds may remain viable for long periods under cold laboratory storage conditions (Billings & Mooney, 1968; Chambers, 1989), little comparative data are available on seed longevities in the natural habitat. The prolonged seed longevities predicted on the basis of our experiments thus are very interesting. Using a similar extrapolation technique and the same negative exponential model we have employed here, Guariguata and Azocar (1988) estimated that seeds of the giant tropical Andean rosette species *Espeletia timotensis* could potentially remain viable in the soil for 4–5 years. *Chionochloa macra* turned out to have a non-persistent seed bank in the alpine region of New Zealand (Spence, 1990). Cavieres and Arroyo (2001) reported that in the Andes of central Chile, seeds

of the perennial herb *Phacelia secunda* remained viable in the soil for more than 3 years, estimating a longevity of 1782 days (> 4 years) in seeds buried at 3400 m a.s.l. The maximum predicted ages for seeds of several Tierra del Fuego alpine species fall well beyond that of *E. timotensis* and *P. secunda*. However, species with shorter longevities were also revealed for our site.

It should be recalled that mathematical fits were only possible for 4 of the 12 species showing potential to form a persistent seed bank. Most of those excluded belong to a group of species in which percent seed viability in the penultimate exhumation date was significantly lower than on the last date, resulting in U-shaped seed viability curves. Notwithstanding, it also turns out that several of the same species in the group that showed anomalous behavior in the Tetrazolium test showed little or no depression in final total viable seeds as measured on the final exhumation date. Consequently, the maximum seed longevities estimated on the basis of curve fitting are probably lower than in several species for which curves could not be developed.

That significant reductions in viability of physically intact seeds were registered mostly on a single observation date (363 days) might indicate a technical problem. However, this is unlikely because many species assayed on that date were not affected, and the experimental protocol was identical for all species. It is well known that some seeds experience an annual dormancy cycle when buried (Baskin & Baskin, 1998) involving profound changes in seed physiology. Changes in basic seed physiology over an annual cycle determining variation in sensitivity to the Tetrazolium test could also be expected. The depression in seed viability registered on the second exhumation date, which was the driest of the three exhumation dates, followed by recuperation of the viability reaction at the later autumn date, is perhaps determined by some aspect of seed physiology eliciting the Tetrazolium reaction that might be altered by late summer–early autumn environmental conditions.

One aspect that cannot be evaluated satisfactorily on the basis of the present information is potential phylogenetic effects. A growing body of evidence has demonstrated strong phylogenetic constraints in flowering phenology (Kocher & Handel, 1986), fruit traits (Herrera, 1992), seed number and mass (Mazer, 1989), and seed longevity (Thompson et al., 1998). Nevertheless, we have tried to avoid the confounding effect of possible phylogenetic constraints on seed longevity in our study by eliminating taxonomic redundancy as much as possible without compromising the need to include the dominant alpine species on the study site. Our data set has no taxonomic redundancy at the generic level, and only two sources of redundancy at the familial level, where the Apiaceae are represented by three genera (*Bolax*, *Azorella*, and *Oreomyrrhis*) and the Ranunculaceae are represented by two genera (*Caltha* and *Anemone*). Perusal of the results suggests that the seed longevities of representatives of Apiaceae are almost as diverse in their seed bank characteristics as the total set of genera considered. The representatives of *Caltha* and *Anemone*, nevertheless, show fairly similar behavior.

Finally, although it is clear that there are still many unknowns surrounding the persistent seed bank biology in alpine habitats in general, our results suggest an important potential to form long-term persistent seed banks (cf. Thompson et al., 1998) in many species of the alpine region of the subantarctic zone of southern Chile. This is in agreement with recent studies (e.g., Cavieres, 1999), which suggest that factors such as the strong inter-annual variation in the length of growing season and the small-scale disturbances in the soil will favor the formation of persistent seed banks in alpine habitats (see also Forbis, 2003). Additionally, the low diversity of both seed predators and pathogenic fungi (McGraw & Vavrek, 1989), and the ambient low temperatures that are associated with low embryonic metabolic rates and slow consumption of seed reserves, favor the seed longevity observed in alpine soils.

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STATISTICAL SUMMARY OF SOME OF THE ACTIVITIES IN THE MISSOURI BOTANICAL GARDEN HERBARIUM, 2003

	Vascular	Bryophyte	Total
Acquisition of Specimens			
Staff Collections	24,234	2,526	26,760
Purchase	0	0	0
Exchange	16,207	2,865	19,072
Gifts	5,255	156	5,411
Total acquisitions	45,696	5,547	51,243
Mountings			
Newly mounted at MO	99,565	24,355	123,920
Specimens mounted when acquired	31,382	n/a	31,382
Repairs			
Specimens repaired	18,183	n/a	18,183
Specimens stamped	1,375	n/a	1,375
Total repairs	19,558	n/a	19,558
Specimens Sent			
On exchange	27,340	489	27,829
As gifts	14,520	1,088	15,608
Total	41,860	1,577	43,437
Loans Sent			
Total transactions	256	35	291
Total specimens	23,850	1,816	25,666
To U.S. institutions			
Transactions	144	16	160
Specimens	14,144	284	14,428
To foreign institutions			
Transactions	112	19	131
Specimens	9,706	1,532	11,238
To student investigators			
Transactions	36	3	39
Specimens	5,109	102	5,211
To professional investigators			
Transactions	220	32	252
Specimens	18,741	1,714	20,455
Loans Received			
Transactions	184	36	220
Specimens	13,171	6,304	19,475

	From U.S.A.	From abroad	Total
Visitors	248	157	405

During 2003, 155,302 specimens were accessioned into the herbarium: 123,920 mounted at MO, 31,382 mounted when acquired, and 1,375 old MO specimens stamped (and numbered). The total number of mounted, accessioned specimens in the herbarium on 1 January 2004 was 5,518,588 (5,087,212 vascular plants and 431,376 bryophytes).

The 31,382 vascular plants listed as "mounted when acquired" are all from the Reed Herbarium, purchased in 2001, and represent about 20 percent of that acquisition.

The Garden's herbarium is closely associated with its database management system, TROPICOS (see ⟨www.mobot.org/mobot/research⟩). The charts below summarize some of the statistics from TROPICOS both for the calendar year 2003 and as year-end totals. Note that the specimen records in TROPICOS are primarily based on MO specimens, meaning that about forty-one percent of the bryophytes (an increase of about three percent over 2002) and thirty-five percent of the vascular plants (an increase of about two percent) in the herbarium are now computerized, with an overall total of about thirty-six percent (an increase of about two percent).

TROPICOS records—Calendar Year 2003 Additions

	Bryophytes	Vascular Plants	Total
Specimens	18,937	129,805	148,742
Names	2,499	20,570	23,069
Synonyms	1,376	10,313	11,689
Distributions	477	24,889	25,366
Types	736	12,765	13,501
Bibliography	1,393	3,857	5,250

TROPICOS records—Year-End 2003 Totals

	Bryophytes	Vascular Plants	Total
Specimens	175,553	1,789,622	1,965,175
Names	106,132	833,232	939,364
Synonyms	69,631	416,862	486,493
Distributions	43,297	848,052	891,349
Types	9,630	304,386	314,016
Bibliography	26,449	70,829	97,278
Specimens in herbarium	431,376	5,087,212	5,518,588
Percent of specimens computerized	41	35	36

In TROPICOS, literature-based Synonymy is always linked to a reference in Bibliography and directly with at least two records in Names, the synonym, often a basionym, and the correct name according to the reference. Additional synonymy may be derived from these direct links, e.g., all other combinations of a basionym treated as a synonym of a given name are also synonyms of it.

—Marshall R. Crosby and James C. Solomon

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CONTENTS

Revisión Taxonómica del Género *Paspalum* Grupo Eriantha (Poaceae, Panicoideae, Paniceae) ——— *Osvaldo Morrone, Silvia S. Denham & Fernando O. Zuloaga* 225

Phylogenetic Analysis of the Madagascan *Euphorbia* subgenus *Lacanthis* Based on ITS Sequence Data ——— *Thomas Haevermans, Petra Hoffmann, Porter P. Lowry II, Jean-Noël Labat & Emile Randrianjohany* 247

Hooglandia, a Newly Discovered Genus of Cunoniaceae from New Caledonia ——— *Gordon McPherson & Porter P. Lowry II* 260

Phylogenetic Position of the New Caledonian Endemic Genus *Hooglandia* (Cunoniaceae) as Determined by Maximum Parsimony Analysis of Chloroplast DNA ——— *Patrick W. Sweeney, Jason C. Bradford & Porter P. Lowry II* 266

Evolution of Veroniceae: A Phylogenetic Perspective ——— *Dirk C. Albach, Ma. Montserrat Martínez-Ortega, Manfred A. Fischer & Mark W. Chase* 275

Cladistic Relationships of *Aechmea* (Bromeliaceae, Bromelioideae) and Allied Genera ——— *Ana Paula Gelli de Faria, Tânia Wendt & Gregory K. Brown* 303

What Is the Taxonomic Status of *Polygonella*? Evidence of Floral Morphology ——— *L. P. Ronse De Craene, S.-P. Hong & E. F. Smets* 320

Pollination Biology of *Aristolochia grandiflora* (Aristolochiaceae) in Veracruz, Mexico ——— *K. S. Burgess, J. Singfield, V. Melendez & P. G. Kevan* 346

Experimental Evidence of Potential for Persistent Seed Bank Formation at a Subantarctic Alpine Site in Tierra del Fuego, Chile ——— *Mary T. Kalin Arroyo, Lohengrin A. Cavieres & Ana María Humaña* 357

Statistical Summary of Some of the Activities in the Missouri Botanical Garden Herbarium, 2003 ——— *Marshall R. Crosby & James C. Solomon* 366

Cover illustration. *Trisetum ligulatum* Finot & Zuloaga, drawn by Vladimiro Dudás.

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POLLINATION ECOLOGY OF *GAURA* AND *CALYLOPHUS* (ONAGRACEAE, TRIBE ONAGREAE) IN WESTERN TEXAS, U.S.A.[1]

Richard R. Clinebell II,[2] *Angela Crowe,*[3] *David P. Gregory,*[4] *and Peter C. Hoch*[2]

Abstract

This analysis reports insect visitors, with pollen load data, for the major flowering species of a plant community at the Monahans Sandhills and nearby sites in the Transpecos region of western Texas, U.S.A., with concentration on four species of Onagraceae, tribe Onagreae. We characterize the pollinators of two species of *Gaura* (*G. coccinea* and *G. villosa*) and two species of *Calylophus* (*C. berlandieri* and *C. hartwegii*), as well as three major co-blooming non-onagrad species (*Thelesperma megapotamicum* (Asteraceae), *Mentzelia strictissima* (Loasaceae), and *Argemone polyanthemos* (Papaveraceae)). Partial data were collected on two additional species of Onagreae, *Oenothera engelmanii* and *O. rhombipetala*. Insect collections were made during repeated visits to the plant community, with sampling throughout the flowering season and a 24-hour period. Nearly 1300 insects were captured on the nine target plant taxa, with more than 100 insect species carrying pollen. The primary species of Onagraceae studied had diverse insect visitors, and different insects served as primary pollen carriers for different species. *Gaura villosa* showed the greatest diversity, with at least 32 insect species carrying pollen, the major carriers being the antlion *Scotoleon*, 2 species of noctuid moths, and 2 halictid bees in *Sphecodogastra*. By contrast, the pollen carriers of *G. coccinea* were noctuid and geometrid moths; of *Calylophus berlandieri* one of the same species of *Sphecodogastra*, several chrysomelid and buprestid beetles

[1] The authors are grateful to Peter H. Raven and Dennis Breedlove for the opportunity to study and analyze their earlier collections of onagrad pollinators for inclusion in this paper and to the National Geographic Society and the Missouri Botanical Garden for fieldwork support. We also gratefully acknowledge prior support for Raven from the U.S. National Science Foundation. We are grateful to the Field Museum for funding research at the Museum by Clinebell and for permission to work with their collections. We thank the following taxonomic specialists for help with insect identifications: Ted MacRae (Monsanto Company) and Philip Parrillo (Field Museum) for Coleoptera; Neil Evanhuis (Bishop Museum) and David Pollock (Bishop) for Diptera; Mike Arduser (Missouri Department of Conservation) and Ron McGinley (Illinois Natural History Survey) for Hymenoptera; Paul Goldstein (Field), Phil Koenig (no affiliation), and Richard Heitzman (no affiliation) for Lepidoptera; and Norm Penny (California Academy of Sciences) for Neuroptera. Robert Raguso (USCH), Warren Wagner (US), and George Yatskievych (MO) provided help with plant identifications. Don Hardin (Washington University) provided assistance in the field, preparation of tables, and photographic documentation. Richard Keating (MO) helped in the preparation of photomicrographs. We are grateful to the library staff of the Missouri Botanical Garden for their generous help in locating and borrowing necessary entomological publications. We also thank Raguso, the editor, and an anonymous reviewer for comments that improved this paper.

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(Coleoptera), and several beeflies (Diptera); and of *C. hartwegii* a combination of the sphingid moth *Hyles lineata*, several noctuid moths, the honeybee *Apis mellifera*, and the same species of *Sphecodogastra*. The 3 co-blooming species also had a diversity of insect visitors, but there was essentially no overlap in major pollen carriers between the species of Onagraceae and the non-onagrads. This report of pollination by antlions is the first unambiguous such report for any member of the order Neuroptera. At least 5 species of antlions visit the flowers of *Gaura villosa*, and *Scotoleon minusculus* is the most important pollen-carrying species for this taxon. All visits by antlions occurred between 10:00 P.M. and 5:00 A.M., which may explain why this phenomenon has not been reported before.

Key words: antlions, *Calylophus*, *Gaura*, Onagraceae, pollination, *Sphecodogastra*.

The plant family Onagraceae provides an excellent model in which to study the evolution of pollination systems. Due largely to the efforts of Raven (1979, 1988) and associates, detailed modern taxonomic revisions are available or in preparation for virtually all species of the family, as are detailed comparative studies of the morphology and anatomy of pollen, stigmas, flowers, seeds, and other reproductive characters (reviewed in Raven, 1979; Hoch et al., 1993). At least preliminary pollination data have been published for many groups, especially *Oenothera* (Gregory, 1963, 1964, including *Calylophus*; Linsley et al., 1964), *Camissonia* (Linsley et al., 1963a, b, 1973; Raven, 1969), and *Clarkia* (MacSwain et al., 1973) in the tribe Onagreae, and Raven (1979) presented a lucid overall synthesis of the reproductive biology of the family. Recent work by Raguso and associates (Raguso & Pichersky, 1995; Raguso & Willis, 2002; Levin et al., 2003a) has begun to document adaptive changes in nectar, floral morphology, visual display, and floral fragrance associated with hawkmoth pollination in Onagraceae and other families, building in part on earlier studies by Gregory (1963, 1964).

An understanding of relationships within Onagraceae (8 tribes, 17 genera, and about 650 species; Raven, 1988; Levin et al., 2003b), which is essential to a comparative study of pollination biology, is beginning to emerge, based on both morphological (Hoch et al., 1993) and molecular phylogenetics (Crisci et al., 1990; Bult & Zimmer, 1993; Conti et al., 1993; Levin et al., 2003b, 2004). Of particular importance to the present study is the strong support for a terminal clade that includes tribes Onagreae (8 genera) and Epilobieae (2 genera; Conti et al., 1993; Levin et al., 2003b). Raven (1964) suggested that *Gaura* and *Calylophus*, two genera of Onagreae, were closely related based on similarities in stigma and anther morphology, a view supported by embryological studies (Tobe & Raven, 1985). Recent phylogenetic analysis of Onagreae based on chloroplast and nuclear DNA sequences (Levin et al., 2003b, 2004) strongly supports a clade of *Calylophus* + *Oenothera* + *Gaura* + *Stenosiphon*, and a close sister-taxon relationship between *Gaura* and *Stenosiphon*, the latter clade also supported by Hoggard et al. (2004). However, *Calylophus* now appears to be more closely related to certain sections of *Oenothera*, and the *Gaura* + *Stenosiphon* clade to other sections of *Oenothera*. Additional study is in progress, using additional nuclear DNA sequences and more extensive sampling within the tribe, since these initial findings challenge the classification of the tribe that has been in place for some 40 years (Raven, 1964, 1979, 1988).

Gaura (21 species; Raven & Gregory, 1972a, b) and *Calylophus* (6 species; Towner, 1977) both occur primarily in the southern plains of the United States and adjacent Mexico, with concentrations of taxa in western Texas. Morphological (Carr et al., 1990) and molecular (Hoggard et al., 2004) phylogenies for *Gaura* are available; those for *Calylophus* are in progress. Both genera are characterized by a diversity of pollination systems. Five species of *Gaura* are reported to be self-pollinating, and of the 16 outcrossing species, 13 are pollinated by small moths, 1 by hawkmoths, and 2 by bees, butterflies, and flies (Raven & Gregory, 1972a; Raven, 1979). One species of *Calylophus* is reported to be autogamous, and of the five outcrossing species, three are visited by hawkmoths (one of these also by various bees), and the other two by bees, beetles, butterflies, and occasional hawkmoths (Towner, 1977; Raven, 1979). The diversity of pollination syndromes found in these genera provides testable hypotheses regarding the evolution of the species and their reproductive biology.

Even in this comparatively well-known tribe Onagreae, much of the information on pollination systems is descriptive or anecdotal and often rests on insect pollinator collections from only one or a few short periods of observation. Few previous studies—in this or most other groups—have documented insect visitors to a plant species through the entire daily and seasonal cycles (Robertson, 1928) nor have many tested the efficacy of those visitors as pollen vectors (Schemske & Horvitz, 1984).

Our study exploits three features of *Gaura* and

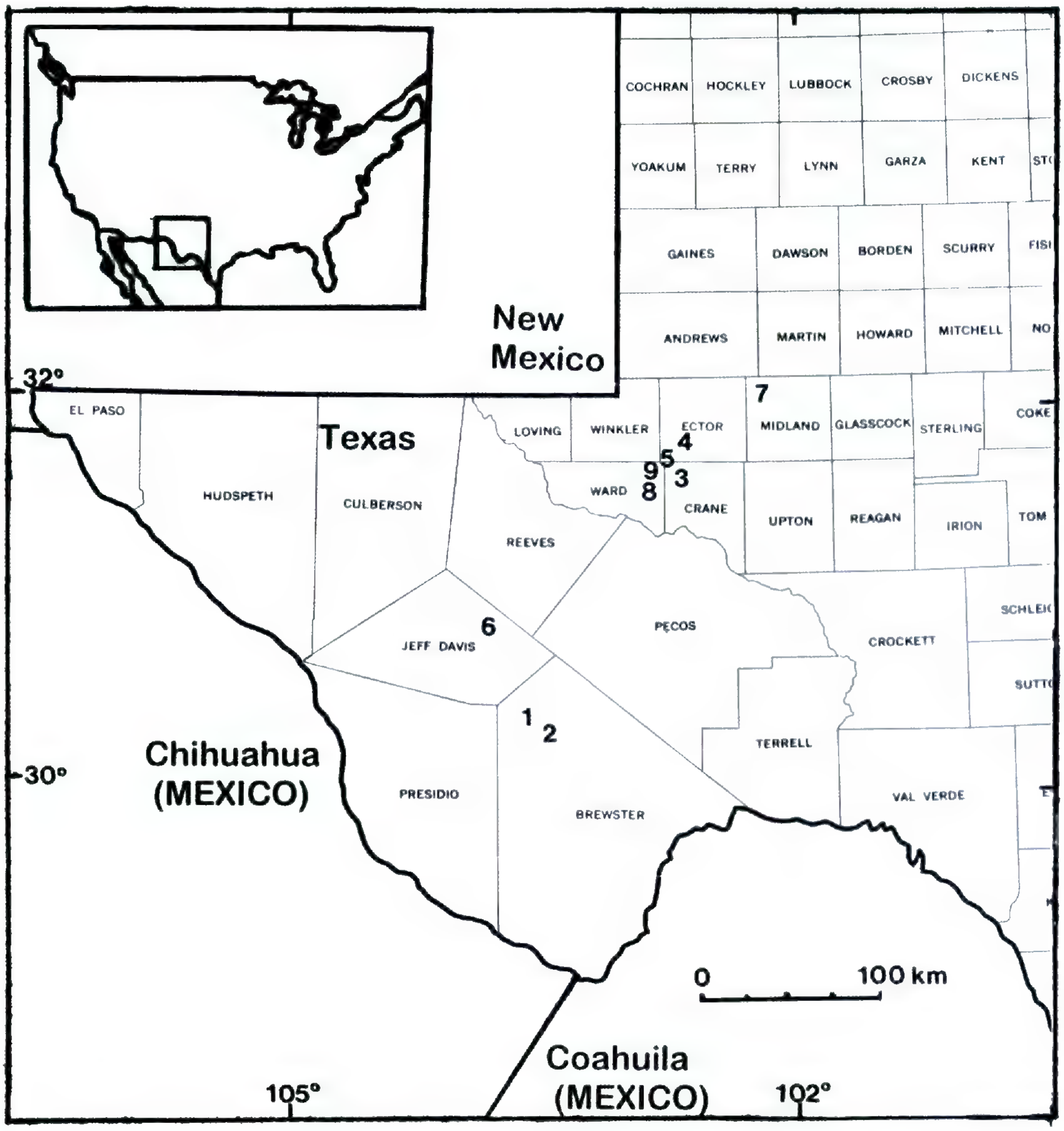

Figure 1. Map of southwestern Texas, U.S.A., with adjacent sections of New Mexico and Mexico (Chihuahua and Coahuila); numbers 1–9 on map refer to study site localities detailed in Table 1.

Calylophus—the existence of a diversity of major pollinators, the availability of sound taxonomies and testable phylogenetic hypotheses, and the occurrence of several related plant taxa in a relatively restricted geographical area—to facilitate the gathering of comparative pollination data and the eco-evolutionary interpretation of these data. Our approach simultaneously considers the patterns of pollinator visitation of several taxa of Onagreae, as well as that of the major co-blooming taxa in other plant families that grow with them. This approach provides data for an entire pollination community, which in turn will facilitate comparison with other communities, for our purposes especially those with similar clusters of Onagreae.

This paper considers the community pollination biology of four common and two uncommon sympatric species of Onagreae and three important co-blooming species in Asteraceae, Loasaceae, and Papaveraceae, in the Monahans Sandhills and surrounding areas in western Texas (Fig. 1; Table 1, with voucher information). Two other species of Onagreae, *Oenothera engelmannii* and *O. rhombipetala*, were present at the site, but attracted few insect visitors (based on limited observations) and may be autogamous. Future papers in this series will include analyses of other communities in the American Southwest rich in representation of species of Onagreae, especially *Gaura* and *Calylophus*, leading ultimately to an evolutionary synthesis for the pollination biology of these groups. Our primary focus here is to describe and quantify the pollinator guilds for a plant community in the Monahans Sandhills that includes a variety of species of Onagraceae, as a step toward analyzing the evolution of pollination biology in Onagraceae tribe Ona-

Table 1. Localities included in this study. All sites are in Texas, U.S.A.; locality numbers coincide with numbers on Figure 1 and are referenced in the text and Tables 4–10. Plant species studied at each locality are noted with vouchers, where available (all specimens deposited at MO except as noted). Plants are in family Onagraceae, except as noted.

1. Brewster Co.: outskirts of Alpine; 2 June 1964
   Gaura coccinea Pursh: *Raven & Gregory 19182* (CAS)
2. Brewster Co.: 16.2 km W Marathon on TX Hwy. 90; 22–28 May 2000
   Calylophus hartwegii (Benth.) P. H. Raven subsp. *filifolius* (Eastw.) Towner & P. H. Raven: *Clinebell 2086*
   Gaura coccinea: *Clinebell 2085*
3. Crane Co.: 20.8 km E Monahans on TX Hwy. 1053; 18 June 1966
   Gaura villosa Torr. subsp. *villosa*: *Gregory s.n.* (RSA)
4. Ector Co.: 22.4 km E Monahans on US Hwy. I-20 frontage road; 1–2 June 1964
   Gaura coccinea: *Raven & Gregory 19234*
   G. villosa subsp. *villosa*: *Raven & Gregory 19235*
5. Ector Co.: 17.2 km E Monahans on US Hwy. I-20 frontage road: 28 May 2000
   Gaura coccinea: *Clinebell*, no voucher
6. Jeff Davis Co.: 9.3 km & 30.4 km S Toyahvale; 16 May 1959
   Gaura coccinea: *Gregory 108–163* (RSA)
7. Midland Co.: W end of Midland; 1 June 1964
   Gaura villosa subsp. *villosa*: *Raven & Gregory 19224* (RSA)
8. Ward Co.: 10.7 km S Monahans, 2 June 1964
   Calylophus hartwegii subsp. *filifolius*: *Raven & Gregory, no voucher*
   Gaura coccinea: *Raven & Gregory 19231* (CAS)
9. Ward Co.: 2–14 km E Monahans on US Hwy. I-20 frontage road; 7–12 June and 30 Aug–1 Sep. 1999; 20–29 May 2000; 6–13 May 2001
   Calylophus berlandieri Spach subsp. *berlandieri*: *Clinebell 2034, 2096*
   C. hartwegii subsp. *filifolius*: *Clinebell 2093, 3066*
   Gaura villosa subsp. *villosa*: *Clinebell 2032, 2036*
   G. coccinea: *Clinebell*, no voucher
   Oenothera engelmannii (Small) Munz: *Clinebell 2040, 3063*
   O. rhombipetala Nutt. ex Torr. & A. Gray: *Clinebell 2031, 2041*
   Asteraceae: *Thelesperma megapotamicum* (Spreng.) Kuntze: *Clinebell 2033*
   Loasaceae: *Mentzelia strictissima* (Wooton & Standl.) J. Darl.: *Clinebell 2039*
   Papaveraceae: *Argemone polyanthemos* (Fedde) G. B. Ownbey: *Clinebell 2037*

greae. As an additional focus, our analysis addresses the debate regarding generalized versus specialized pollination, using the community pollination ecology of the Monahans site.

Materials and Methods

The data presented here utilize pollinator collections made by D. Breedlove, D. Gregory, P. Raven, and H. Towner in 1959–1966 throughout North America on *Gaura* (Raven & Gregory, 1972a, b) and in the early 1970s on *Calylophus* (Towner, 1977). Many of those results were reported anecdotally in those monographs. One of us (RC) extended these studies on both genera starting in 1998. We have combined these data sets into several biogeographically meaningful units (Table 1), of which the data set presented here is the first.

Most of the earlier data were collected between 7:00 P.M. and midnight, resulting in specimen collections strongly weighted toward noctuid and sphingid moths, which are both active primarily at dusk. Subsequent observations revealed the importance of other pollinator groups that are active during other times of the day and night. In order to render the analysis random or unbiased with regard to time of day, recent fieldwork has emphasized these other times of pollinator activity, with relatively less sampling from 7:00 P.M. to midnight. Relative amounts of time devoted to pollinator capture by time of day are presented in Table 2.

Within any time period, we tried to randomize sampling of floral visitors in recent fieldwork. The insect-capture technique employed multiple nets and killing jars, each dedicated to one plant species. The collector(s) alternated among the different net-jar combinations, which enabled more or less continuous collecting, avoided delays while the insects were asphyxiated in the jars, kept the samples collected on each plant species separated, and resulted in more equal sampling times among plant

Table 2. Cumulative hours spent collecting pollinators at each plant species by time period and average number of insects caught per hour of observation. In some cases, we collected insects from more than one plant species during the same time period, as explained in the text.

	12 A.M. TO 4 A.M.	4 A.M. TO 8 A.M.	8 A.M. TO 12 P.M	12 P.M. TO 4 P.M.	4 P.M. TO 8 P.M.	8 P.M. TO 12 A.M.	Total observation hours	Average # insects caught/ observation hour
Gaura villosa	8	15	9	3	9	20	64	8.6
Calylophus berlandieri	8	15	8	6	10	12	59	4.3
Gaura coccinea			2		2	14	18	13.2
Calylophus hartwegii		1			2	9	12	6.5
Thelesperma megapotamicum		1	3	4	9	1	18	3.1
Mentzelia strictissima		4	6		6	7	23	1.8
Argemone polyanthemos		4	6		6	7	23	3.1
Oenothera rhombipetala						6	6	
Oenothera engelmannii		2	5	2		2	11	
Totals	16	42	39	15	44	78	ΣΣ = 234	

species. A primary set of insect specimen vouchers is maintained at the Missouri Botanical Garden, with duplicate sets deposited at the California Academy of Science, the Enns Museum at the University of Missouri, the Field Museum, the Smithsonian Institution, and the Snow Entomological Museum at the University of Kansas. Clinebell visited the Field and Snow museums to consult their collections.

Pollen load analysis involved bathing the insects in ethanol, or removing pollen from corbicular or scopal provisioning loads, and making permanent slides stained with basic fuchsin (Calberla's solution; Clinebell & Bernhardt, 1998). Pollen loads were then identified with the aid of a pollen reference library (at MO), consisting of similarly prepared slides for each of the plant species blooming at the site. Pollen of Onagraceae is highly distinctive due to its shape, "paracrystalline beaded" ektexine, and viscin threads (Raven, 1988; Hoch et al., 1993), and even in mixed pollen loads we were able to distinguish among specific taxa of *Calylophus*, *Gaura*, and *Oenothera* using pollen size, shape, and apertural outline, as described by Praglowski et al. (1987, 1988). In order to simplify the tables and facilitate comparisons among individuals and sites, we grouped pollen loads into five size classes, with the largest being simply "> 500 grains." In order to calculate total amounts of pollen carried by species and overall, we used the mean of each size class (i.e., 1–10 grains—mean 5; 11–50—mean 30; 51–100—mean 75; 101–500—mean 300; and > 500—estimate 500), multiplied times the number of individuals in that class.

In addition to determining overall pollen load on individual insects, we tried to note the pattern of pollen deposition and specifically where on the insect body the pollen was found. Coupled with observation of insect behavior in the course of floral foraging, this pattern may provide useful data regarding the efficacy of the insect as a pollinator. In all cases we recorded total pollen present on captured insects.

In listing Lepidoptera (moths and butterflies) in our tables, we have followed most standard references on North American moths (Covell, 1984; Holland, 1968), while acknowledging that the accepted higher classification of some groups such as the Catocalinae has been modified quite substantially (Poole, 1989). According to Hepner's (1998) classification of Lepidoptera, all of the moths we encountered belong to suborder Glossata, cohort Myoglossata, division Ditrysia. Within this group, all except the Pyralidae (sect. Tineina) belong to section Cossina, subsection Bombycina. McGinley's (2003) recent monograph of the halictid bee genus *Sphecodogastra* proved most useful for that group, as did Penny et al. (1997) for the Neuroptera in our sample. Determinations for most insect groups were provided or checked by authorities as listed in the acknowledgments.

The collection protocol, large sample sizes, and pollen load analysis are intended to ensure that our methods will include the major pollen carriers for each species of plant studied. This in turn enables accurate delimitation of both similarities and differences in the pollinator guilds serving each plant species. When sufficient data were available, we tested the statistical significance of pollinator

Table 3. Selected floral characters related to pollination biology for species of Onagraceae in this analysis; measurements (mm) listed are the mean of measurements made on five individuals from the primary study population. Measurements in parentheses are from descriptions provided in revisions for *Calylophus* (Towner, 1977), *Gaura* (Raven & Gregory, 1972a), and *Oenothera* (Dietrich & Wagner, 1988).

Taxon	Floral tube			Distance from throat to longer anthers	Distance from throat to stigma	Petal length
	Length of cylindrical part	Length of flaring apex	Diameter at throat			
Calylophus berlandieri	4.8 (3–11)	5.6 (2–9)	7.0 (3–14)	7.8 (2–11)	8.2 (4–10)	15.2 (6–25)
Calylophus hartwegii	19.2 (11–33)	11.6 (5–17)	5.5 (4–14)	7.6 (6–13)	12.8 (8–12)	12.6 (12–23)
Gaura coccinea	5.0 (4–11)	N/A —	2.3 —	5.0 (3–7)	7.0 (6–10)	5.0 (3–8)
Gaura villosa	2.4 (1.5–5)	N/A —	2.0 —	6.9 (4–11)	8.1 (7–13)	4.3 (7–13)
Oenothera rhombipetala	29.0 (30–45)	N/A —	5.0 —	15.0 (13–23)	25.0 (15–25)	20.0 (15–35)

choice using Chi-square test for independence (Conover, 1980), where similar pollinators seemed to be choosing different onagrads to visit in their foraging activities. The null hypothesis predicts that insect groups should visit different plants equally during their respective times of flower-visiting activity.

Behavioral observations are necessary to separate those carriers of pollen that might be expected to effect pollination from those that do not. In terms of logistics, it is difficult to collect and observe simultaneously. While our characterization of the pollinator guilds is quantitative, our behavioral observations are, by their nature, qualitative. Behavioral observations often are sufficient to separate pollinators from non-pollinators, but may not be sufficient to evaluate the relative efficacies of various pollinators. We tried to combine collection and observation at all study sites.

One challenge in this study is that all groups of insect visitors are not equally likely to be captured. In three instances, our field activities unwittingly baited insects that are included in our data. (1) The onagrad oligolege *Sphecodogastra noctivaga* is largely nocturnal on *Gaura villosa*, and because these bees are small and hard to see at night, most were captured secondarily in net sweeps for moths. However, Gregory collected a large set of this species (including many females carrying onagrad pollen) under the dome light of his car while parked at a *Gaura villosa* colony in the Monahans Sandhills, and we have included these data in our analysis. (2) Colorful, orange and black beeflies (*Poecilanthrax effrenus*) are regular diurnal visitors to both *Calylophus berlandieri* and *Thelesperma megapotanicum*, but due to their extremely fast and unpredictable flight, they are almost impossible to catch in the act of foraging, and few were actually captured on flowers. On several occasions, however, large numbers of these beeflies were captured when they landed on nets, clothing, and skin, apparently attracted by a concentration of onagrad secondary compounds. Most of these insects carried either *Calylophus* or *Thelesperma* pollen, and were assigned to these respective species in the tables. The few beeflies that lacked pollen loads have been assigned to *Calylophus*, since they appear to have been attracted by volatiles of that species. In general, it is our assumption that baiting is a legitimate part of scientific sampling, especially for documenting relative abundances of such a diverse community of floral visitors as reported here. (3) Whereas five species of antlions were captured on *Gaura villosa* flowers, the only two males of *Brachynemurus hubbardi* were collected at the car dome light. However, both carried *Gaura* pollen, so we included them in our analysis even though they were not caught actually visiting flowers.

FLORAL FEATURES AND PHENOLOGY

Table 3 summarizes floral measurements of particular relevance to pollination for the taxa of Onagraceae in this analysis, with mean measurements from our study populations as well as overall ranges of measurements for the species. Five taxa (both species of *Gaura*, *Calylophus berlandieri*, *Argemone polyanthemos*, and *Mentzelia strictissima*) were in full bloom from early May through early September, while only a few flowers were present on *Theles-*

Figure 2. Habitat in Monahans Sandhills, Ward Co., Texas (site 9, Table 1); typical dune vegetation; 1 Sep. 1999 (photo by D. Hardin).

perma megapotamicum in late August through early September. Both species of *Oenothera* were in bloom on only one of the four field trips to the site made by Clinebell: *Oenothera engelmannii* was in full bloom in early May 2001, and *O. rhombipetala* only in early June 1999.

STUDY AREAS

All of our study sites are located in an area bounded roughly by 30.2–32.1°N, 102–103.8°W, in Brewster, Crane, Ector, Jeff Davis, Midland, and Ward Counties of southwestern Texas, U.S.A. (Table 1; Fig. 1). Our primary sites occur within the Monahans Sandhills eco-geographic region (Fig. 2); the other sites are located in the adjacent Transpecos region (between the Pecos and Rio Grande Rivers). Elevations of these sites range from about 800 to 1400 m.

The Monahans Sandhills are a young feature of the Pecos Plain (about 16,000 years old; Machenberg, 1984), bordering the Caprock Escarpment along the western border of the Llano Estacado, or southern high plains of south-central North America. The sandhills formation extends along this escarpment, which trapped the sand on its leeward side, about 50 to 100 km east of the Pecos River. The dune formations extend northwesterly from the Monahans dunefields through about 250 km of southeastern New Mexico, and range from 20 to 60 km across, from east to west. Their formation is associated with paleowinds from the northwest and the arid conditions that accompanied the close of the most recent ice age (Machenberg, 1984).

The preservation of a section of the sandhills formation stems from the publication of Bedichek's (1947) *Adventures with a Texas Naturalist*, which inspired local support for protection beginning in 1957. Today, 1554 hectares of the sandhills have been preserved as Monahans Sandhills State Park (Ward Co., Texas), which features both active and stabilized dunes. This park, located about 8 km to the west of Monahans bordering U.S. Highway I-20, and its immediate surroundings served as our primary study site (site 9, Table 1; Fig. 2). Because the park is closed at night when many onagrad pollinators are active, our study areas were adjacent to the park along the frontage roads on both sides of I-20. These areas contain many fine coppice dunes, which are stabilized by the miniature shin oak (*Quercus havardii* Rydb.). Other woody plants commonly encountered include honey mesquite (*Prosopis glandulosa* Torr.) and desert willow (*Chilopsis linearis* (Cav.) Sweet). Major grasses include xeric species of *Andropogon*, *Calamovilfa*, *Eragros-*

tis, and *Panicum*; cacti and *Yucca* are also abundant (Machenberg, 1984). Embedded in this matrix is a rich diversity of forbs, of which the species studied are the most abundant from late May to early September. Nearby secondary study areas (sites 3–5, 7–8) are similar.

On a map, the dunal areas appear as islands on the Pecos plains. In the dunal areas themselves, species of Onagraceae commonly encountered include *Calylophus berlandieri*, *Gaura villosa*, and *Oenothera rhombipetala*. On interdunal sites, the common onagrads are *Calylophus hartwegii*, *Gaura coccinea*, and *G. villosa*.

The sites in Transpecos Texas (sites 1, 2, 6 in Brewster and Jeff Davis Counties, about 100 km southwest of the Monahans Sandhills) include more arborescent elements of mesquite savanna, and are rich in *Gaura coccinea* and *Calylophus hartwegii*. Here, the onagrad species typical of the dunes were absent. Overall, the mosaic character of the sandhill belt is such that it is not unusual to find these key onagrads in various random subsets, depending upon local variation in substrates. Additional species of Onagreae are present in southwestern Texas, but we believe that the ones chosen for this analysis represent a majority of the pollination syndromes of Onagreae that occur in the Transpecos and Permian Basin (area to the east of the Pecos River, and of which the sandhills are a part).

Results

Insect visitors were collected throughout the day and night from nine species of plants in southwestern Texas, including six species of Onagreae (Tables 1, 2). We present data on Onagraceae first, followed by other families, and within Onagraceae list species in order of decreasing size of visitor samples.

Gaura villosa Torr. subsp. *villosa*

Gregory studied this self-incompatible perennial species in the sandhills region (sites 4 and 7 in June 1964 and site 3 in June 1966). His collections, made between about 8:00 P.M. and midnight, are included with Clinebell's data from site 9 in 1999–2001, which were recorded in additional discrete time intervals. Almost every moth collected at site 4 on 2 June 1964 contained *Gaura* pollen on the proboscis, whereas a similar collection of moths made at site 7 on 1 June 1964 less than 50 km away contained almost no *Gaura* pollen; these latter account for many of the "no *Gaura* pollen" individuals of the two most abundant noctuid moth foragers, *Bulia deducta* and *Melipotis indomita* (underwing subfamily, Catocalinae). A collection of 46 pollinators made at site 9 on 30 Aug.–1 Sep. 1999 is combined with data from May to June, since the two data sets include comparable groups of pollinators. We collected additional pollinators at site 9 on 6–13 May 2001. Extreme drought marked the years 1999 and 2000, whereas the winter of 2001 was very wet, producing remarkable flowering displays throughout western Texas.

As summarized in Table 4, we captured a total of 562 insect visitors belonging to 45 species on *Gaura villosa*. In terms of individual visits, the 27 species of Lepidoptera account for a majority (353 visits; 63% of the total) followed by the 6 species of Neuroptera (128; 23%), and the 7 species of Hymenoptera (68; 12%); visits by Coleoptera (3 species) and Diptera (2 species), mostly without pollen, are negligible. The most numerous visitors by species are the noctuid moth *Bulia deducta* (253; 45%), the antlion *Scotoleon minusculus* (104; 18%), the noctuid *Melipotis indomita* (46; 8%), and 2 species of the halictid bee *Sphecodogastra* (each 27; 5%). We estimate that these 562 individuals carried some 32,705 pollen grains. In terms of pollen carried, the importance of the Lepidoptera is diminished relative to the other two groups: Neuroptera account for gross pollen load of 20,045 grains (61%), Hymenoptera for 8720 (27%), and Lepidoptera for only 4035 (12%). The species that cumulatively carry the largest pollen loads are the antlion *Scotoleon minusculus* (18,160 grains; 55%), the halictid bee *Sphecodogastra danforthi* (4345 grains; 13%), the noctuid moth *Bulia deducta* (2130 grains; 6%), the bee *Sphecodogastra noctivaga* (1755 grains; 5%), and the introduced honey bee *Apis mellifera* (1500 grains; 5%). So although noctuid moths collectively appear to be important pollinators of *Gaura villosa*, the antlion *Scotoleon* and the two species of *Sphecodogastra* bees are the major pollen carriers for this species, responsible for nearly three-quarters of the total pollen load in this analysis.

The activity of these major pollinators spans the entire time of day and night during which *Gaura villosa* flowers were open. In the 1960s, Gregory began collecting pollinators as early as 7:45 P.M. and ceased sampling around midnight. In the drought years of 1999 and 2000, the flowers opened later, after 10:00 P.M. In May 2000, we clocked the opening of the first flowers at 10:35 P.M. The flowers, which last only one day, then remained open for several hours after sunrise (a few as late as 10:00 A.M.).

Most of the insects collected from anthesis to midnight were noctuid moths in the subfamily Ca-

tocalinae, especially *Bulia deducta* and *Melipotis indomita*. In the drought years, these were joined around midnight by a variety of winged adult antlions, especially *Scotoleon minusculus* (of both sexes), but also including four other species of antlions. In the non-drought year of 2001, *Gaura villosa* flowers opened about 9:00 P.M., and moths and antlions were encountered foraging together from 9:30 P.M. until morning. Throughout the night, onagrad oligoleges in the sweat bee family Halictidae (*Sphecodogastra noctivaga*, both sexes) were also collected, mostly in sweeps for moths. After sunrise, another halictid oligolege, *Sphecodogastra danforthi*, actively foraged for pollen on both the *Gaura* and nearby *Calylophus berlandieri*. This species was collected at *Gaura* flowers in both May–June and August–September observational periods, and sometimes carried mixed loads of *Gaura* and *Calylophus* pollen. *Sphecodogastra danforthi* remained active until about 9:30 A.M. Another halictid bee and onagrad oligolege, *Evylaeus* sp. 1, was also collected in the morning on *Gaura*. While this species is not abundant in this data set, it is well represented in another collection made at the Kiowa National Grassland (Union County, New Mexico, U.S.A.) in July 1999 (Clinebell, unpublished data), where *Sphecodogastra danforthi* was not collected.

Linsley and MacSwain (1962) reported *Sphecodogastra texana* and *S. noctivaga* as geographical replacements, with *S. texana* occurring largely to the east of the Monahans Sandhills and *S. noctivaga* to the west. Those authors reported the two species as sympatric from the sandhills alone, but all specimens in our collection key to *S. noctivaga*. Ecologically, these two species are similar and unique within *Sphecodogastra* in that they are the only known nocturnal species in the genus, which is otherwise crepuscular or matinal; this includes *S. danforthi* in our analysis.

CALYLOPHUS BERLANDIERI SPACH SUBSP. *BERLANDIERI*

Like *Gaura villosa*, this self-incompatible onagrad taxon has a long blooming period from March to September throughout Texas, western Oklahoma, and adjacent regions (Towner, 1977). Clinebell studied this species in June and August–September 1999, May 2000, and May 2001 at the Monahans Sandhills (site 9, Table 1). All study populations grew intermixed with *Gaura villosa*. Anthesis of this species occurs shortly before sunrise (Towner, 1977) when the halictid bee *Sphecodogastra danforthi* begins to forage. This bee species remains active only from sunrise until about 9:30 A.M., but accounts for almost half of the sample of pollinators (Table 5). In early morning, but continuing throughout the day, pollen-eating beetles visit the flowers; the most common beetles are the buprestid *Achmaeodera mixta* and the chrysomelid genus *Altica* (*Altica* sp. indet.). As the day progressed, beeflies in five genera of Bombylidae, especially *Heterostylum robustum* and *Poecilanthrax effrenus*, visited the flowers. Two large anthophorid bees, in the genera *Centris* and *Diadasia*, visited rarely; only a single individual of each was collected. In early May 2001, the halictid bee *Sphecodogastra danforthi* was infrequent, and the major early morning pollinator was the bombyliid beefly *Poecilognathus scolopax*.

We recorded 252 individuals representing 27 insect species visiting the flowers of *Calylophus berlandieri*, and carrying a total pollen load of 52,010 grains (Table 5). In order, the most important groups are as follows: Hymenoptera (7 species, 106 individuals (42%), carrying 44,240 grains (85%)); Coleoptera (10 species, 80 individuals (32%), carrying 4650 grains (9%)); Diptera (5 species, 60 individuals (24%), carrying 2940 grains (6%)); and the Lepidoptera and Neuroptera, both of negligible importance as visitors and carriers. The halictid bee *Sphecodogastra danforthi*, which is also a significant pollen carrier of *Gaura villosa* (Table 4), accounts for 40% of the individual visits, but nearly 83% of the cumulative pollen load of *Calylophus berlandieri*. Several other species of beetles, beeflies, and larger bees are significant visitors to this plant, but none of them carry more than 5% of the total pollen load recorded. Because of the slight herkogamy of the flowers of this species, virtually all floral visitors are true pollinators, regardless of whether they are visiting the flowers for pollen, for nectar, or for both. Seasonal variation in the pollinator guild appears minimal in our data set. Towner's (1977) list of floral visitors in Potter Co., Texas, is a qualitative subset of our collection.

GAURA COCCINEA PURSH

Both Gregory and Clinebell studied this self-incompatible species in both the Monahans Sandhills (sites 4 and 8 and sites 5 and 9, respectively) and in mesquite savanna (sites 1 and 6 and site 2, respectively) in Transpecos Texas (Table 1). In 1964 and 1959, Gregory commenced collecting moths at about 7:00 P.M., whereas in the drought year of 2000 the flowers opened later, between 9:00 and 9:30 P.M. This pattern of delayed anthesis is similar to the pattern reported above for *Gaura villosa* in the drought years of 1999 and 2000. At sites 5 and

Table 4. Floral foragers on *Gaura villosa* subsp. *villosa* in the Permian Basin (Texas, U.S.A.: see Table 1 for site data); pooled data from 1–2 June 1964 (sites 4, 7); 18 June 1966 (site 3); 7–12 June, 30 Aug.–1 Sep. 1999, 20–29 May 2000, and 6–13 May 2001 (site 9). Legend: F = female; M = male; W = worker; a = *Argemone polyanthemos*; b = *Mentzelia strictissima*; c = *Calylophus berlandieri*; d = *Asclepias* sp. pollinia.

	No. *Gaura* pollen	1 to 10 *Gaura* grains	11 to 50 *Gaura* grains	51 to 100 *Gaura* grains	101 to 500 *Gaura* grains	>500 *Gaura* grains	Other pollen carried	Totals
Coleoptera								
Cantharidae								
Chauliognathus sp.	1							1
Chrysomelidae								
Altica sp. indet. 1	7	1						8
Diabrotica undecimpunctata Mann.	1							1
Diptera								
Bombyliidae								
Poecilanthrax effrenus (Coquillett); M	1							1
Tachinidae sp. indet. 1	1							1
Hymenoptera								
Andrenidae								
Perdita sp. indet 1; F		1						1
Apidae								
Apis mellifera L.; W						3		3
Halictidae								
Agapostemon angelicus Cockerell; F				1				1
Agapostemon splendens (Lepel.); F		1						1
Evylaeus sp. 1; F	1	1	1			2	a(1), b(1)	5
Evylaeus sp. 1; M	3							3
Sphecodogastra noctivaga (Linsley & MacSwain); F	13	1	5		2	2		23
Sphecodogastra noctivaga (Linsley & MacSwain); M	4							4
Sphecodogastra danforthi McGinley; F	5	2	2	1	4	6	b(1), c(1)	20
Sphecodogastra danforthi McGinley; M	6	1						7
Lepidoptera								
Butterflies								
Pieridae								
Nathalis iole; M	2							2
Moths								
Arctiidae sp. indet. 1	1							1
Geometridae								
Semiothisa punctilineata (Packard)	1							1
Geometrid sp. indet. 1	1	1						2
Noctuidae								
Acontiinae								
Acontia aprica (Hubner)	2							2
Amphipyrinae								
Cosmia calami (Harvey)			1					1
Catocalinae								
Bulia deducta (Morr.)	155	54	37	6	1		d(3)	253
Caenurgina erechtea (Cram.)				1				1
Melipotis indomita Wlk.	24	12	4	4	2			46
Melipotis jucunda Hubner		2	1					3
Syneda howlandi Grote; M				1				1
Hadeninae								
Pseudaletia unipunctata (Haw.)		1						1

Table 4. Continued.

	No. *Gaura* pollen	1 to 10 *Gaura* grains	11 to 50 *Gaura* grains	51 to 100 *Gaura* grains	101 to 500 *Gaura* grains	>500 *Gaura* grains	Other pollen carried	Totals
Heliothinae								
Helicoverpa zea (Boddie)	2	3						5
Schinia gaurae (J. E. Smith); M		1	1					2
Noctuinae								
Agrotis malefida Guenee	6	1	1					8
Feltia volubilis Harvey	1							1
Plusiinae								
Trichoplusia ni (Hbn.)				1				1
noctuid sp. indet. 1 (small, white)			1					1
noctuid sp. indet. (12 mm, mottled brown)			2					2
noctuid sp. indet. (15 mm, mottled brown)		1						1
noctuid sp. indet. (12 mm, light tan)					1			1
Pyralidae								
Achyra rantalis (Guenee)	8	2						10
Nomophila nearctica Monroe	1							1
Sphingidae								
Hyles lineata L.			1					1
moth sp. indet. (light brown)	4							4
moth sp. indet. (small, cream)	1							1
moth sp. indet. (small, tan)	1							1
Neuroptera								
Chrysopidae								
lacewing sp. indet. 1	1	1						2
Myrmeleontidae								
Brachynemurus hubbardi; M		1	1		2			4
Brachynemurus hubbardi; F	1	2	1	1				5
Paranthaclisis hageni; F	3	3			2			8
Paranthaclisis hageni; M	1		1	1				3
Scotoleon minusculus N. Banks; F	1	1	8	10	31	7		61
Scotoleon minusculus N. Banks; M	2	3	17	11	10			13
Vella fallax; M (60 mm)		1						1
antlion sp. indet. 1; M (40 mm)					1			1
Totals	262	101	85	38	56	20		ΣΣ = 562

9, Clinebell collected early morning bees on this species that are similar at least at the family level to those collected in the llanos of San Luis Potosí, Mexico, by Breedlove (collections at the Missouri Botanical Garden, analyzed by Clinebell), and dissimilar to morning bees collected on *G. villosa* and *Calylophus berlandieri* as discussed previously.

The 238 individuals collected on *Gaura coccinea* represent 34 species of insects (Table 6), and they carry a cumulative pollen load of 4945 grains. Although Coleoptera, Diptera, and Hymenoptera were present, all were negligible in importance compared with the Lepidoptera, especially geometrid and noctuid moths, which account cumulatively for 86% of the individual visits and 99% of the gross pollen load. The noctuid moth *Bulia deducta* was marginally the most important species in terms of individuals (57, 24%) and pollen carried (830 grains, 17%), but at least four other moth species (*Melipotis indomita, M. jucunda, Discestra trifolii,* and an undetermined species) carried nearly as much pollen (Table 6).

The noctuid moths *Bulia deducta* and *Melipotis indomita* are major floral visitors to both *Gaura coccinea* and *G. villosa,* but *G. coccinea* also attracts a wider array of other small noctuids and geometers in the first two hours after anthesis (Table 6). We have not yet studied *Gaura coccinea* between midnight and sunrise, so we do not know if antlions play a role in its pollination. A number of bees that

Table 5. Floral foragers on *Calylophus berlandieri* subsp. *berlandierei* in the Monahans Sandhills (Texas, U.S.A.: site 9, Table 1); pooled data from 7–12 June, 30 Aug.–1 Sep. 1999, 20–29 May 2000, and 6–13 May 2001. Legend: F = female; M = male; a = *Thelesperma megapotamicum*; b = *Mentzelia strictissima*; c = *Mimosa quadrivalvis* var. *occidentalis*; d = *Gaura villosa*; e = *Argemone polyanthemos*. Counts designated with an asterisk (*) are from slides made to quantify proportions of mixed loads of *Calylophus* and *Gaura* pollen. Specimens often carried much larger loads (> 1000 grains) of *Calylophus* pollen.

	No *Caly.* pollen	1 to 10 *Caly.* grains	11 to 50 *Caly.* grains	51 to 100 *Caly.* grains	101 to 500 *Caly.* grains	>500 *Caly.* grains	Other pollens carried	Totals
Coleoptera								
Buprestidae								
Achmaeodera mixta			6	1	4	2	a(2)	13
Cantharidae								
Chauliognathus sp. indet. 1			1					1
Chrysomelidae								
Altica sp. indet. 1	15	12	16	4	3		b(2)	50
Cleridae								
Trichodes oresterus Wolcott		1	1				a(2)	2
Coccinellidae								
lady beetle sp. indet. 1	1							1
Meloidae								
Eupompha viridis (Horn)	2	1	1					4
Scarabaeidae								
Anomala sp. indet. 1		1						1
Euphoria sp. indet. 1 (black and yellow)					1			1
beetle sp. indet. 1 (black, 4 mm)	2	4						6
beetle sp. indet. 2 (orange-brown, 5 mm)			1					1
Diptera								
Bombyliidae								
Anastoechus sp indet.; M	1							1
Exoprosopa sp. indet.	3						a(2)	3
Heterostylum robustum (Osten Sacken); F			3	1	5			9
Poecilanthrax effrenus (Coq.)	6	10	9				a(8)	25
Poecilognathus scolopax (Osten Sacken)	4	5	6	6	1			22
Hymenoptera								
Anthophoridae								
Centris caesalpiniae Clell.; F						1	b(1)	1
Diadasia rinconis; M				1			b(1)	1
Apidae								
Bombus pennsylvanicus (DeGeer); W						1	c(1)	1
Halictidae								
Evylaeus sp. indet. 1		1						1
Sphecodogastra danforthi McGinley; F	1			4	10*	80*	d(13)	95
Sphecodogastra danforthi McGinley; M	2	2						4
Sphecodogastra lusoria (Cresson); F	2							2
Tiphiidae								
Tiphia sp. indet. 1; F	1						b(1)	1
Lepidoptera								
Danaidae								
Danaus gilippus (Cramer); F	1						e(1)	1
Hesperiidae								
Lerodea eufola (W. H. Edwards)	1							1
Lycaenidae								
lycaenid sp. indet 1	1							1
Noctuidae								
Plusiinae								
Autographa biloba (Stephens)			1					1
Pieridae								
Nathalis iole; M	1							1
Neuroptera								
Myrmeleontidae								
Scotoleon minusculus N. Banks; F	1							1
Totals	45	37	45	17	24	84		ΣΣ = 252

are otherwise rare in our data set visit this species in the early morning, but most of these bees, including the anthophorid *Martinapis enteicornis* (both sexes) and the halictid *Agapostemon angelicus* (males only), carry little or no pollen. Considering the relatively high number of insect visitors to this species, the total pollen load identified is considerably smaller than those for other species of Onagraceae in this analysis. It is unclear if we have missed one or more major pollen carriers, or if this species relies more heavily on insect visitors like noctuid moths or small bees that individually carry small pollen loads but that are present in large numbers.

CALYLOPHUS HARTWEGII (BENTH.) P. H. RAVEN SUBSP. *FILIFOLIUS* (EASTW.) TOWNER & P. H. RAVEN

Just as we often encountered *Calylophus berlandieri* and *Gaura villosa* together on the sandiest sites, we also noted an association between *C. hartwegii* and *G. coccinea* on firmer substrates. Gregory studied the self-incompatible *C. hartwegii* at site 8 in the Monahans area; Clinebell studied it at both Monahans (site 9) and in the Transpecos area (site 2). This species seems to be particularly negatively impacted by drought; at site 9 it bloomed abundantly in 2001, but was not even observed in the drought years of 1999 and 2000. At site 2 in the drought year of 2000, it did bloom, but the first flowers did not open until 8:00 P.M., at least a half an hour later than the same plants in the mesic year of 2001.

During each evening of observation, anthesis in *Calylophus hartwegii* set off a "rush" of activity by sphinx moths. The first sphingid moths (*Hyles lineata*) appeared at 8:15 P.M., and the last at 9:20 P.M. We also collected the large noctuid moths *Bulia* and *Melipotis* here, but they were notably less abundant on *Calylophus* than on *Gaura* at the same sites. At site 2, about a third of the 54 floral visitors were worker honeybees (*Apis mellifera*), which were otherwise uncommon in the data set. By comparison, honeybees (and noctuid moths) did not visit this taxon at Monahans (site 9). This underscores a great problem for students of southwestern pollination biology: where feral honeybees are abundant, their presence may affect adversely the activities of native insects (Primack & Silander, 1975). The presence of honeybees may be less of a problem in the case of sphingid moth-pollinated species like *Calylophus hartwegii*, where honeybees and sphingid moths co-forage in apparent harmony, possibly by partitioning nectar versus pollen resources. However, in the case of diurnal bee-pollinated taxa like *C. berlandieri* or *C. tubicula* (Towner, 1977), presence of honeybees negatively impacts the native bees. At a population of *C. tubicula* in Brewster County, Texas, near Big Bend National Park, honeybees were the major visitor and pollen carrier, competitively excluding the native bees that are present and presumably are the original pollinators (Clinebell, unpublished data; see also Towner, 1977). We interpret the lack of noctuid moth visitation on *C. hartwegii* at Monahans to the abundance at the site of *Gaura villosa*, a preferred noctuid nectar resource. By contrast, at the Brewster County site, there were few *G. coccinea* plants versus many *C. hartwegii* plants, rendering any resource partitioning between the noctuid and sphingid moths bioenergetically untenable.

As summarized in Table 7, 77 individuals representing 13 species were captured on *Calylophus hartwegii*, carrying a total of 11,665 pollen grains. Lepidoptera account for most of the individuals recorded (50, 65%), compared to Hymenoptera (23, 30%), with Coleoptera and Neuroptera present, but of negligible significance. However, Hymenoptera carry a majority of the pollen load (7530 grains, 65%), compared to Lepidoptera (4130 grains, 35%). The sphingid moth *Hyles* is the most common visitor (27 individuals, 35%; with 3535 grains, 30%), especially at Monahans (site 9), but overall carries less pollen than the introduced honeybee *Apis* (18, 23%; with 5500 grains, 47%), which occurs only at site 2. The next most abundant visitors are noctuid moths *Bulia* (7 individuals, 9%) and *Melipotis* (5, 6%) and the native halictid bee *Sphecodogastra danforthi* (5, 6%), but in terms of pollen loads, the latter carries significantly more pollen (2030 grains, 17%) than the noctuids (both 140 grains, 1%). In fact, the single individual of the large sphingid moth (*Manduca quinquemaculata*) encountered carried more pollen (300 grains, 3%) than all of the noctuid moths combined. It appears that all of the Hymenoptera reported on *C. hartwegii* are pollen robbers rather than pollinators, as they do not contact the stigmas during their foraging, whereas the sphingid moths always made contact. Similarly, the noctuids also appear to be largely nectar robbers. Thus, only the sphingid moths were effective pollinators, due to the extreme herkogamy of the flowers.

Most of the pollen of *Calylophus hartwegii*, a self-incompatible species, was moved by sphingid moths (*Hyles lineata*) at Monahans, and at other sites by sphingids and honeybees, with smaller amounts of pollen carried by the noctuid moths *Bulia deducta* and *Melipotis indomita* (Table 7). Gregory (1964) also studied this taxon (as *Oenothera*

Table 6. Floral foragers on *Gaura coccinea* from sites in Texas, U.S.A. (see Table 1 for site data); pooled data from 7 and 16 May 1959 (site 6); 1–2 June 1964 (sites 1, 4, 8); and 22–28 May 2000 (site 9). Legend: a = *Dalea* sp.; b = *Mimosa quadrivalvis* var. *occidentalis*; c = *Asclepias* sp. *pollinia*.

	No *Gaura* pollen	1 to 10 *Gaura* pollen	11 to 50 *Gaura* pollen	51 to 100 *Gaura* pollen	101 to 500 *Gaura* pollen	>500 *Gaura* pollen	Other pollens carried	Totals
Coleoptera								
Buprestidae								
Achmaeodera mixta	1						a	1
Chrysomelidae								
Altica sp. indet. 1	7	4						11
Cleridae								
Trichodes oresteres Wolcott	1							1
Diptera								
Bombyliidae								
Poecilognathus scolopax (Osten Sacken)	4							4
Hymenoptera								
Anthophoridae								
Martinapis enteicornis (Clell.); F		1						1
Martinapis enteicornis (Clell.); M	2	3	1				a(5), b(1)	6
Halictidae								
Agapostemon angelicus Cockerell; M	7	3						10
Lepidoptera								
Moths								
Geometridae								
Semiothisa sp. indet. 1 (small, tan)	14	19	9	5				47
Scotogramma infuscata Smith	1							1
geometrid sp. indet. 1 (18 mm, brown)	1	1	1					3
Noctuidae								
Acontiinae								
Acontia aprica (Hubner)	1							1
Acontia sp. indet. 1 (5 mm, brown)	6	1						7
Acontia sp. indet. 2 (8 mm, black & tan)	2							2
Cobubatha orthozona (Hampton)	1							1
Catocalinae								
Bulia deducta (Morr.)	29	13	13	1	1		c(2)	57
Matigramma rubrosuffusa Grote		2						2
Melipotis indomita Wlk.		3	16	3				22
Melipotis jucunda Hubner	1	1	6			1		9
Hadeninae								
Discestra trifolii (Hufnagel)					1			1
Leucania sp. indet. 1		1	1					2
hadeninid sp. indet. (15 mm, with brown reticulations)				1				1
Heliothinae								
Helicoverpa zea (Boddie)	2	4	4	2				12
Schinia citrinella		1	1					2
Noctuinae								
Agrotis malefida Guenee			1					1
noctuinid sp. indet. 1			1					1
Plusiinae								
Rachiplusia ou (Guenee)				1				1
moth sp. indet. 1 (small, tan)		1	1					2
moth sp. indet. 2 (small, brown)		1						1
moth sp. indet. 3 (small, tan with brown markings)	7	4	2	1	2			16

Table 6. Continued.

	No *Gaura* pollen	1 to 10 *Gaura* pollen	11 to 50 *Gaura* pollen	51 to 100 *Gaura* pollen	101 to 500 *Gaura* pollen	>500 *Gaura* pollen	Other pollens carried	Totals
moth sp. indet. 4 (13 mm, dark brown)			1	1				2
Pyralidae								
Pyraustinae								
Pyraustinae sp. indet. 1			1					1
Diatsictis fracturalis (Zeller)	3							3
Epipagis huronalis (Guenee)	2	1	1					4
pyralid sp. indet. 1 (13 mm, reddish)	1							1
Sphingidae								
Hyles lineata L.	1							1
Totals	94	64	60	15	4	1		ΣΣ = 238

hartwegii) in the Monahans area. He described visitation by large bees in *Melissodes* (Anthophoridae) and *Megachile* (Megachilidae) in the hour before sunset, and anecdotally ascribed to bees the majority of the pollen transfer. We did not observe these bees visiting *C. hartwegii* in our studies in the same general region. Instead, we found these large bees on *Argemone polyanthemos* (Table 10), and in no cases did they carry any onagrad pollen.

We include here observations of two additional species of Onagraceae tribe Onagreae that occurred sporadically at the Monahans site 9 (Table 1). However, these species were not present in sufficient numbers to allow us to analyze their pollination biology completely.

OENOTHERA RHOMBIPETALA NUTT. EX TORR. & A. GRAY

Clinebell studied this species in June 1999 at Monahans (site 9) with *Calylophus berlandieri* and *Gaura villosa* on stabilized dunes, but blooming plants were absent in the severe drought year 2000. During a fairly short observational period of six hours (Table 2) in 1999, he collected three sphingid moths (*Hyles lineata*), three noctuid moths (*Melipotis indomita*), and a beetle (*Eupompha viridis* Horn). This anecdotal information suggests that *O. rhombipetala*, with long corolla tubes (2.5–3 cm long), is pollinated primarily by sphingid moths, much like *C. hartwegii*, which also possesses long corolla tubes.

OENOTHERA ENGELMANNII (SMALL) MUNZ

Clinebell observed this species at Monahans in 1999 and 2000, but the plants were never in bloom. In May 2001, however, *O. engelmannii* bloomed abundantly. In the course of several hours of observation in early morning and early evening, few insects visited its flowers. Additional fieldwork is needed for this species.

In addition to the six onagrads just discussed, Clinebell collected floral visitors on three taxa that bloomed at the same time in these communities: *Thelesperma megapotamicum* (Asteraceae), *Mentzelia strictissima* (Loasaceae), and *Argemone polyanthemos* (Papaveraceae; Table 1). We include them in the analysis as part of a community-ecology approach to the study of Onagraceae pollination, in order to identify flower-visiting insects shared with the onagrad taxa as well as those that do not come to the onagrads. These three non-onagrad species co-occurred with *Calylophus berlandieri* and *Gaura villosa* in the stabilized dune areas of site 9 (Table 1; Fig. 2).

THELESPERMA MEGAPOTAMICUM (SPRENG.) KUNTZE

Commonly known as Navajo tea, this species of Asteraceae was abundant in the stabilized dunes and attracted numerous beeflies and scoliid wasps. A total of 56 insects in 22 species carried a cumulative load of 10,950 pollen grains (Table 8). The colorful orange and black beefly *Poecilanthrax effrenus* was the most common visitor (15 individuals, 27%) and carried much of the pollen moved (3390 grains, 31%). This beefly divided its time between Navajo tea and the onagrad *Calylophus berlandieri*. The single individual encountered of the large beefly, *Anthrax* sp. indet. (at 15 mm long, as large as a small bumblebee), also carried a large load of *Thelesperma* pollen. The next most abundant pollen carrier was another beefly, *Exoprosopa* sp. 1 (11 individuals, 20%), which carried 760 pollen grains (7%). The

Table 7. Floral foragers on *Calylophus hartwegii* subsp. *filifolius* in the Permian Basin and Transpecos region (Texas, U.S.A.: see Table 1 for site data); pooled data from 2 June 1964 (site 8); 22–28 May 2000 (site 2); and 6–13 May 2001 (site 9). Legend: F = female; M = male; W = worker; a = *Dalea* sp.; b = *Gaura villosa*; c = Solanaceae or Nyctaginaceae; asterisks (*) refer to sight records, pollen load unknown.

	No *Caly.* pollen	1 to 10 *Caly.* grains	11 to 50 *Caly.* grains	51 to 100 *Caly.* grains	101 to 500 *Caly.* grains	>500 *Caly.* grains	Other pollens carried	Totals
Coleoptera								
Chrysomelidae								
Altica sp. indet. 1	2	1						3
Hymenoptera								
Apidae								
Apis mellifera L.; W	7*					11	a(2), b(1)	18
Halictidae								
Sphecodogastra danforthi McGinley; F			1			4		5
Lepidoptera								
Moths								
Noctuidae								
Acontiinae								
acontiinid sp. indet. 1 (brown, 7 mm)	3							3
Catocalinae								
Bulia deducta (Morr.)	3	1	2	1				7
Drasteria pallescens (Grote & Robinson)		1						1
Matigramma rubrosuffosa Grote		1						1
Melipotis indomita Wlk.	1	1	2	1				5
Heliothinae								
Shinia citrinella (Grote & Robinson)	3	1						4
Pyralidae								
Diastictis fracturalis (Zeller)	1							1
Sphingidae								
Hyles lineata L.	7*	2	5	5	5	3	c(1)	27
Manduca quinquemaculata (Haworth)					1		c	1
Neuroptera								
Myrmeleontidae								
Scotoleon minusculus (N. Banks); M	1							1
Totals	28	8	10	7	6	18		Σ = 77

third most common pollen carrier, which was encountered nowhere else in this data set, was the small orange-yellow scoliid wasp *Trielis octomaculata* (4 individuals, 7%), carrying the second largest amount of pollen (2000 grains, 18%). Two individuals of an undetermined wasp carried the third largest cumulative pollen load (1000 grains, 9%). At least 11 different insect species carried significant loads of *Thelesperma* pollen (> 100 grains), many of them represented in the data set by only a single specimen (such as the beefly *Anthrax*).

MENTZELIA STRICTISSIMA (WOOTON & STANDL.) J. DARL.

A sample of 42 floral visitors in 11 species, carrying a cumulative pollen load of 16,790 grains and collected at site 9 in June and Aug.–Sep. 1999 (Table 1), shows no significant overlaps between this species of Loasaceae and any co-blooming onagrads (Table 9). Bees accounted for most of the visitors (35 individuals, 83%) and carried most of the pollen (16,025 grains, 95%); only one beefly (Diptera; 2% pollen carried), one skipper (Hesperiidae; Lepidoptera), and five beetles (Coleoptera; 2% pollen carried) were collected on *Mentzelia*. The co-dominant visitors to *M. strictissima* are worker bumblebees (*Bombus pennsylvanicus*) and females of the green halictid bee *Agapostemon splendens*, each with 10 individuals (24%) that carry cumulatively 5000 grains (30%) each. Both species are rare else-

Table 8. Floral foragers on *Thelesperma megapotamicum* (Asteraceae) in the Monahans sandhills (Texas, U.S.A.: site 9, Table 1); pooled data from 7–12 June, 30 Aug.–1 Sep. 1999, 28 May 2000, and 6 May 2001. Legend: F = female; M = male; a = *Mimosa quadrivalvis* var. *occidentalis*; b = *Argemone polyanthemos*; c = *Calylophus berlandieri*.

	No *Thele.* pollen	1 to 10 *Thele.* grains	11 to 50 *Thele.* grains	51 to 100 *Thele.* grains	101 to 500 *Thele.* grains	>500 *Thele.* grains	Other pollens carried	Totals
Coleoptera								
Cleridae								
Thrichodes oresterus Wolcott						1		1
Chrysomelidae								
Diabrotica undecimpunctata Mann.			1					1
coleopteran sp. indet. 1 (gray)			1					1
Diptera								
Bombyliidae								
Anthrax sp indet. 1						1		1
Chrysanthrax edititius (Say)			1	1				2
Exoprosopa sp. indet. 1	1	5	2	1	2			11
Exoprosopa sp. indet. 2				1				1
Poecilanthrax effrenus (Coquillett); M				1	2	1		4
Poecilanthrax effrenus (Coquillett); F					1			1
Poecilanthrax effrenus (Coquillett); M+F			3	3	2	2		10
Bombyliid sp. indet. 1		1						1
Syrphidae								
Eristalis sp. indet. 1					1			1
Tachinidae sp. indet. 1				1	2			3
Hymenoptera								
Halictidae								
Agapostemon angelicus Cockerell; M		2						2
Sphecodogastra danforthi McGinley; F						1		1
Ichneumonidae								
ichneumonid sp. indet. 1			1					1
Scoliidae								
Trielis octomaculata texensis (S. ss.); M						1		1
Trielis octomaculata texensis (S. ss.); F						3	a(2), b(1)	3
Sphecidae								
Sphex sp. indet. 1; F						1		1
Vespidae								
Eumeninae sp. indet. 1; M						1		1
wasp sp. indet. 1; M						2	a(1)	2
Lepidoptera								
Lycaenidae								
lycaenid sp. indet. 1 (small, blue)	1							1
Nymphalidae								
Euptoieta claudia (Cramer)		2	1				c(1)	3
Pieridae								
Colias philodice philodice Godart; F	1							1
Nathalis iole Bois.; F	1							1
Totals	4	10	10	8	10	14		ΣΣ = 56

where in our data sets. *Perdita kiowi*, a small cream-colored andrenid bee that is active at twilight and well-camouflaged on the *Mentzelia* blooms, is found nowhere else in our collections.

ARGEMONE POLYANTHEMOS (FEDDE) G. B. OWNBEY

This species intergrades considerably with *Argemone albiflora* Hornem. subsp. *texana* G. B.

Table 9. Floral foragers on *Mentzelia strictissima* (Loasaceae) in the Monahans sandhills (Texas, U.S.A.: site 9, Table 1); pooled data from 7–12 June 1999 and 30 Aug.–1 Sep. 1999. Legend: F = female; M = male; W = worker; a = *Argemone polyanthemos*.

	No *Ment.* pollen	1 to 10 *Ment.* grains	11 to 50 *Ment.* grains	51 to 100 *Ment.* grains	101 to 500 *Ment.* grains	>500 *Ment.* grains	Other pollens carried	Totals
Coleoptera								
coleopteran sp. indet. 1 (11 mm, gray)	1		3		1			5
Diptera								
Bombyliidae								
Poecilognathus scopulax (Osten Sacken); F			1					1
Hymenoptera								
Andrenidae								
Perdita kiowi Griswold; M	2							2
Perdita kiowi Griswold; F			1	1				2
Apidae								
Apis mellifera L.; W				4				4
Bombus pennsylvanicus (DeGeer); W				10			a(2)	10
Halictidae								
Agapostemon angelicus Cockerell; F				1				1
Agapostemon splendens (Lepel.); F				10				10
Agapostemon splendens (Lepel.); M				3				3
Augochloropsis sumptuosa (Smith); F				1			a(1)	1
Dialictus sp. indet. 1; F				1				1
Evylaeus sp. indet. 1; F	1							1
Lepidoptera								
Hesperiidae								
Atalopedes campestris huron W. H. Edwards; M				1				1
Totals	1		3	4	3	31		Σ = 42

Ownbey (Papaveraceae) in central Texas, and although the two are considered to be distinct species, these white prickly poppies are often not easily separable (Diggs et al., 1999). We have treated the specimens from the Monahans Sandhills (site 9) as *A. polyanthemos*. Most of the 72 floral visitors in this sample, belonging to 18 species and cumulatively carrying 27,140 pollen grains (Table 10), show no overlap with the insects sampled on Onagraceae. Hymenoptera account for most visitors (56, 78%) and most pollen carried (23,895 grains, 88%), with Coleoptera (10, 14%; 2405 grains, 9%) and Diptera (5, 7%; 930 grains, 3%) also present. Females of the anthophorid bee *Diadasia rinconis* are unique to *Argemone* in the data set, though one also carried some *Mentzelia* pollen. Both males (20 individuals, 28%) and females (11, 15%) of this cactus bee were the most common *Argemone* pollen carriers; altogether, *Diadasia rinconis* carried 13,100 grains (48%). One male and two female long-tongued megachilid bees (*Megachile monti-vaga*) carrying significant pollen loads (≥ 300 grains each) also were unique in the data set, as were two other species of *Megachile*. The halictid bee *Augochloropsis sumptuosa* was otherwise found only on *Mentzelia*. We collected four individuals (6%) of *Evylaeus* sp. 1, another halictid bee commonly encountered on species of Onagraceae; notably, one of the specimens captured on *Argemone* had a pollen load with 90% *Gaura* pollen. The anthophorid and megachilid bees were mostly collected in early morning, sleeping in the flowers in the crevice between the stamen cluster and the petals, often in groups. Since the stigma of this species is located at the center of the ball of stamens, these bees would have to crawl to the top of the stamen ball before flying off in order to effect pollination, and this was not observed. However, this spatial arrangement of stigma and stamens applies to all floral visitors, and we have no observations that would single out one group of visitors as being more or less effective as pollinators.

Table 10. Floral foragers on *Argemone polyanthemos* (Papaveraceae) in the Monahans Sandhills (Texas, U.S.A.: site 9, Table 1); pooled data from 7–11 June 1999 and 6–8 May 2001. Legend: M = male; F = female; a = Onagraceae; b = *Calylophus berlandieri*; c = *Mentzelia strictissima*; d = *Gaura villosa*.

	No *Arge.* pollen	1 to 10 *Arge.* grains	11 to 50 *Arge.* grains	51 to 100 *Arge.* grains	101 to 500 *Arge.* grains	>500 *Arge.* grains	Other pollens carried	Totals
Coleoptera								
Chrysomelidae								
Altica sp.			1					1
Diabrotica undecimpunctata Mann.				1				1
Coccinellidae								
coccinellid sp. indet. 1	1						a	1
Meloidae								
Eupompha viridis (Horn)					4	1		5
coleopteran sp. indet. 1 (red thorax)					2			2
Diptera								
Bombyliidae								
Poecilognathus scopulax (Osten Sacken)					1		b	1
bombyliid sp. indet. 1 (tiny, wings clear)	1							1
Syrphidae								
Eupeodes volucris Osten Sacken; F					2			2
Eupeodes volucris Osten Sacken; M			1					1
Hymenoptera								
Anthophoridae								
Centris atripes Moes.; M					1			1
Diadasia aff. *diminuta* (Cr.); F					1	3		4
Diadasia rinconis Clell.; F	1				3	7	c(1)	11
Diadasia rinconis Clell.; M					5	15		20
Halictidae								
Augochloropsis sumptuosa (Smith); F						2		2
Evylaeus sp. indet. 1; F				1		3	c(1), d(1)	4
Sphecodogastra danforthi McGinley; F			1					1
Megachilidae								
Megachile cf. *laurita*; F					1	4		5
Megachile montivaga Cresson; F						2		2
Megachile montivaga Cresson; M					1			1
Megachile mucurosa Clell.; F						1		1
Megachile mucurosa Clell.; M					2	2		4
Lepidoptera								
Noctuidae								
Plusiinae								
Autographa biloba (Stephens)	1							1
Totals	4		3	2	23	40		Σ = 72

SUMMARY OF MAJOR POLLEN CARRIERS

For this analysis, we define major pollen carriers as insects carrying more than 50 pollen grains of a given plant species; Table 11 lists those major carriers for each of the seven plant species for which we have enough data. For convenience, Table 12 pools major pollen carriers by plant species and shows that there is great specificity in each pollen guild. What is remarkable about these tables is the significant absence of overlap among the major pollen carriers in terms of the plant species they visit. These are unexpected results that argue for the need to conduct more field studies in pollination biology at the community level. Although it has been difficult to get insect determinations across this data set and tedious to quantify the pollen loads, we feel that these data demonstrate a higher level of pollinator specialization in these commu-

Table 11. Major pollen carriers by plant species, defined as any insect carrying more than 50 pollen grains of that plant species. Insect taxa represented in the data set by a single specimen ("singleton") are marked with an asterisk (*) and included in the closest inclusive taxon in which they can be determined.

	Gaura villosa	*Calylophus berlandieri*	*Gaura coccinea*	*Calylophus hartwegii*	*Thelesperma mesopotamicum*	*Mentzelia strictissima*	*Argemone polyanthemos*
Coleoptera						1*	
Buprestidae							
Achmaeodera mixta		7					
Cleridae					1*		
Chrysomelidae							1*
Altica sp. indet. 1		7					
Meloidae							
Eupompha viridis							5
Scarabaeidae		1*					
Coleoptera sp. indet. 1							2
Diptera							
Bombyliidae					3*		
Exoprosopa sp. indet. 1					3		
Heterostylum robustum		6					
Poecilanthrax effrenus					12		
Poecilognathus scopulax		7				1	1
Syrphidae					1*		
Eupeodes volucris							2
Tachinidae indet. 1					3		
Hymenoptera							
Apidae							
Apis mellifera	3			11		4	
Bombus pennsylvanicus		1				10	
Andrenidae							
Perdita kiowi						4	
Anthophoridae		2*					1*
Diadasia aff. *diminuta*							4
D. rinconensis							30
Halictidae						1*	
Agopostemon angelicus	1					1	
A. splendens						13	
Augochloropsis sumptuosa						1	2
Evylaeus sp. indet. 1	2					1	4
Sphecodogastra danforthi	11	94	4	1			
S. noctivaga	4						
Megachilidae							
Megachile montivaga							3
M. mucurosa							5
M. cf. *laurita*							5
Scoliidae							
Trielis octomaculata					4		
Sphecidae					1*		
Vespidae					1*		
wasp indet.					2		
Lepidoptera						1*	
Geometridae							
Semiothisa sp. indet.	5						

Table 11. Continued.

	Gaura villosa	*Calylophus berlandieri*	*Gaura coccinea*	*Calylophus hartwegii*	*Thelesperma mesopotamicum*	*Mentzelia strictissima*	*Argemone polyanthemos*
Noctuidae	4*		5*				
Bulia deducta	7		2	1			
Helicoverpa zea			2				
Melipotis indomita	6		3	1			
noctuid sp. indet. 3			3				
Sphingidae				1*			
Hyles lineata				13			
Neuroptera							
Myrmeleontidae	1*						
Brachynemurus hubbardi	3						
Paranthaclisis hageni	3						
Scotoleon minusculus	69						
Total: singletons	5	3	5	1	7	3	2
Total: all major pollen carriers	114	125	20	31	32	38	65

nities than expected, based on current debate regarding specialized versus generalized pollination niches (Waser et al., 1996). In summarizing pollinator activity (Table 13), we found that the guild fidelity of the seven main plant species ranges from 75.0% to 99.2%, with a mean of 91.2%. Pollen transport efficiency ranged from 8.4% to 90.5% in the seven taxa, with a mean of 50.9% efficiency (the overall "community efficiency" is 33.3%), suggesting considerable variability among species.

At the other extreme, many rare insect species also appear in this large data set. Whether it is the large scarab flower beetle *Euphoria* on *Calylophus berlandieri*, the large antlion *Vella fellax* on *Gaura villosa*, or the large beefly *Anthrax* on *Thelesperma megapotamicum*, these insect rarities represent an

Table 12. Pollination guilds of major pollen carriers for each of the primary plant species in this analysis, as detailed in Table 11. Insect taxa (including singletons) are assigned to the guild of the plant whose pollen they primarily carry (i.e., serve as modal pollen carrier); individual insects that are major pollen carriers for other (non-modal) plant species appear under those species. The halictid bee *Agopostemon angelicus* (only one individual each on *Gaura villosa* and *Mentzelia strictissima*) is assigned to Guild 6 (of *Mentzelia*) because that individual carried a larger load and Guild 6 also includes *A. splendens*.

	Gaura villosa	*Calylophus berlandieri*	*Gaura coccinea*	*Calylophus hartwegii*	*Thelesperma megapotamicum*	*Mentzelia strictissima*	*Argemone polyanthemos*
Guild 1 (*Gaura villosa*)	97		5	2			
Guild 2 (*Calylophus berlandieri*)	11	124		4	1	1	1
Guild 3 (*Gaura coccinea*)			15				
Guild 4 (*Calylophus hartwegii*)	3			25		4	
Guild 5 (*Thelesperma megapotamicum*)					31		
Guild 6 (*Mentzelia strictissima*)	1	1				31	
Guild 7 (*Argemone polyanthemos*)	2					2	64

Table 13. Community summary statistics. The overall community pollen transport efficiency (marked *) is an average for all insect visits observed; this figure is biased by the unequal pollinator sample sizes among the plant species. The mean guild pollen transport efficiency (marked **), the average of the efficiency figures for each of the seven guilds, is not biased by unequal sample sizes.

	Total modal major pollen carriers A	Total floral visitors B	Total non-modal major pollen carriers C	Guild fidelity (%) A/(A+C)	Guild pollen transport efficiency (%) (A+C)/B
Gaura villosa	97	562	17	85.1	20.3
Calylophus berlandieri	124	252	1	99.2	49.6
Gaura coccinea	15	238	5	75.0	8.4
Calylophus hartwegii	25	77	6	80.6	40.3
Thelesperma megapotamicum	31	56	1	96.9	57.1
Mentzelia strictissima	31	42	7	81.6	90.5
Argemone polyanthemos	64	72	1	98.5	90.3
	ΣΣ = 394	ΣΣ = 1299	ΣΣ = 38	91.2	33.3*
				Mean guild pollen transport efficiency:	50.9**

important secondary outcome to the randomized field collection of a sufficiently large sample of the common pollen carriers to enable statistical analysis of the data. These data also highlight the importance of setting aside large areas of natural refuges for the sake of rare species that exist at relatively low population densities, yet play important roles in the pollination biology and ecology of natural communities.

Discussion

We divide the discussion into two parts: (1) foraging behavior of major pollinating insect groups, and comparison with other pollination studies of Onagreae, and (2) analysis of mixed pollen loads carried by foraging insects. Within these areas of discussion, we examine and compare three interrelated themes: (1) geographic replacement of related pollinators across the range of a plant species; (2) the effect of the presence or absence of large numbers of honeybees at a particular site; and (3) the importance of the ecological integrity of the community. The first two themes were highlighted in the Results section to underscore their high importance, and the third theme underpins this entire analysis. The communities studied here represent the most ecologically intact study areas that could be located for these plant species, and represent relicts of the original (i.e., pre-European settlement) vegetation. Pollination studies conducted in degraded areas may well yield different results than those reported here.

1. Foraging behavior of major pollinating groups

We discuss these in a diurnal sequence beginning at sunrise. We note especially those cases where a given insect is a true pollinator in one species of onagrad, but not of other species.

Halictid bees (Hymenoptera) that are onagrad oligoleges

At least three species of *Sphecodogastra* and *Evylaeus* visit onagrad species in the Monahans Sandhills. *Sphecodogastra noctivaga,* the largest (12 mm long) halictid, visits only *Gaura villosa,* mostly from midnight to 6 A.M., but occasionally until 8 A.M. Both sexes of this species are unique among insect visitors to *G. villosa* in that they spent the evenings on the inflorescences, crawling about and resting. They are highly attracted to lights, and were collected by both Gregory and Clinebell at car lights adjacent to colonies of *G. villosa.* Males did not appear to carry any pollen, and females often carried small pollen loads; however, females occasionally carried large amounts of pollen in a full rear femoral scopal load for the provisioning of young. The efficacy of *S. noctivaga* as a pollinator is not known because we were unable to observe their behavior on flowers due to darkness. All bees collected of this species carry only *Gaura villosa* pollen.

We collected *Sphecodogastra danforthi* on *Gaura villosa* and *Calylophus berlandieri* (both Onagraceae). These halictid bees forage on *G. villosa,* where they were found almost exclusively in the

morning, from sunrise until about 9:30 A.M. *Sphecodogastra danforthi* was also infrequently captured at dusk on both species of *Calylophus*. This species is much more prevalent on *C. berlandieri*, accounting for about 40% of individuals (and 83% of pollen carried) of the pollinator data set for that species, than on *Gaura*, where it accounts for about 5% of visitors (and 13% of pollen carried). This halictid bee is an effective pollinator of *Calylophus berlandieri*, frequently climbing over the stigma while traveling from stamen to stamen. It appears to be less effective on *Gaura villosa*, however, due to the more pronounced herkogamy in the latter species, where the stamens (6.5–13.5 mm and clustered in the lower quarter of the zygomorphic flower) are notably separated from the stigma (atop the style 10–18.5 mm; Raven & Gregory, 1972a). Nevertheless, we observed females using the stigma as a landing platform several times, and so pollination might be effected occasionally. Of 135 individuals of *Sphecodogastra danforthi* in the overall data set, 18 carried no onagrad pollen, but only 2 were captured on non-onagrad taxa, 1 each on *Argemone* and *Thelesperma*, carrying pollen of those species. Fourteen individuals carried mixed loads of *Calylophus* and *Gaura* pollen, 13 of which were captured on *Calylophus* flowers. Thus, the 2 *Sphecodogastra* halictid bees, 1 nocturnal and 1 matinal, exhibit an overwhelming preference for foraging on species of Onagraceae.

Evylaeus sp. 1 is not as common in the data set as *Sphecodogastra*, but females do carry onagrad pollen loads. *Evylaeus* lacks the hooked scopal hairs of *Sphecodogastra* (a synapomorphy for the genus; McGinley, 2003) that presumably provide better pollen adherence for that genus. Most of the specimens were captured on *Gaura villosa* from 6:30 to 8:30 A.M., and these foraged with *Sphecodogastra danforthi*. It is doubtful that *Evylaeus* is a reliable pollinator for *G. villosa* for the same reasons stated above for *Sphecodogastra*. Of 13 individuals collected in this study, 4 were found on *Argemone*, and so this halictid bee is not as closely associated with Onagraceae as are the 2 species of *Sphecodogastra*.

To summarize, females of *Sphecodogastra noctivaga* appear to be major effective pollinators of *Gaura villosa* (pending verification by ethological observations); *Sphecodogastra danforthi* is an effective pollinator of *Calylophus berlandieri*, but probably not of *G. villosa*; and *Evylaeus* sp. 1 may not be an effective pollinator of either onagrad species and does not even visit *Calylophus* flowers. *Evylaeus* is uncommon in this data set, and understanding its role at the Monahans Sandhills may require an even larger sample size than reported here, as is also the case for other rare species in the data set.

We tested the null hypothesis that *Sphecodogastra danforthi* and *S. noctivaga* randomly visited flowers of *Calylophus berlandieri* and *Gaura villosa* using the Chi-square test for independence (Conover, 1980). While most individual floral visitors were females, the test was calculated first using both male and female bees. The Chi-square test statistic was 61.31 ($P \ll 0.01$), indicating significant non-random (selective) flower visitation. The test statistic for females only was 60.69 ($P \ll 0.01$), again indicating significant deviation from expectation. These tests scored the bees according to the plant species on which they were collected. Because 17 of the female *Sphecodogastra danforthi* collected on *Calylophus* carried mixed loads of *Calylophus* and *Gaura* pollen, a test was run assigning half of these mixed-load bees to *Gaura*. The resulting test statistic, 46.83 ($P \ll 0.01$), was still highly significant. While collecting efforts began at 7:00 A.M., after which time few *Sphecodogastra danforthi* were collected on *Gaura*, there obviously was an earlier period of activity that included floral visitation to *Gaura*. Whether or not this included a significant number of females that visited only *Gaura* and had ceased foraging before 7:00 A.M. is unknown. A conservative interpretation of these data suggests that *Sphecodogastra noctivaga* does not visit *Calylophus* at all, that females of *Sphecodogastra danforthi* visit both plant taxa, and that these data may be biased in terms of under-representing visits to *Gaura* by *Sphecodogastra danforthi*, if indeed these female bees are more likely to visit *Gaura* than *Calylophus* prior to 7:00 A.M.

Gregory collected most individuals of *Sphecodogastra noctivaga* in this data set in June 1964 around the dome light of a car parked beside a population of *Gaura villosa*, and most of these females carried either no *Gaura* pollen or sparse pollen loads. However, in August 2001, we collected ca. 30 female *S. noctivaga* bees on *G. villosa* in the Cimarron National Grassland (Morton Co., Kansas, U.S.A.), all carrying large *Gaura* pollen loads (unpublished). These are the only active nocturnal pollen foragers on *G. villosa* at both sites. (The other nocturnal floral visitors, noctuid moths and antlions, actively harvest only nectar, but passively transport pollen as a byproduct of nectar foraging.) By contrast, *S. noctivaga* appears from our data to be less abundant at the Monahans Sandhills in Texas, and it is likely that *S. danforthi* visits both onagrad taxa in the presence of low densities of *S. noctivaga* and for whatever reasons, visits *Gaura*

before *Calylophus*. Clinebell collected a large set of male *S. noctivaga* on 22 July 1999 from 1:30 to 3:30 A.M. on the Kiowa National Grassland, Union County, New Mexico. Here, the males carried virtually no pollen, and appeared to be searching for females on *Gaura* inflorescences. We emphasize that *G. villosa* was in bloom in this data set from earliest May to early September, and that while the insect groups collected at Cimarron, Kiowa, and Monahans were the same from site to site, the relative abundances of these groups varied according to site and season. The most dramatic seasonal shift observed was the rarity of *Sphecodogastra danforthi* in early May 2001 at Monahans on flowers of *C. berlandieri*. While pollinator activity always occurred in early morning, the major pollinator in the absence of *S. danforthi* was the small beefly, *Poecilognathus scolopax*.

Clearly, pollen load analysis has been essential for elucidating the complexities of pollinator foraging choice, especially when the pollen grains of related onagrad genera can be distinguished (Praglowski et al., 1988). Without such analysis, we might have concluded (erroneously) that *Sphecodogastra danforthi* does not visit flowers of *Gaura villosa* when in fact it does, but only prior to 7:00 A.M.

A single female of *Sphecodogastra danforthi* was collected on *Thelesperma* and carried a full load of its pollen. Four females of *Evylaeus* sp. 1 were collected on *Argemone*, half of which were also carrying *Gaura* pollen. Otherwise, all pollen found on these halictid bee genera was from Onagraceae flowers.

Halictid bees (Hymenoptera) that are not onagrad oligoleges

Three green halictid bee species included in this data set were not major onagrad pollen carriers at the Monahans Sandhills in Texas. *Agapostemon splendens* (both males and females) occurred primarily on *Mentzelia strictissima*, comprising about one-third of the 42 insect visitors collected on that species. All carried substantial loads of *Mentzelia* pollen. Males of *Agapostemon angelicus* were common on flowers of *Gaura coccinea* in early morning at Monahans, but carried little or no pollen. Singleton females of *A. angelicus* were collected on *Gaura villosa* and *Mentzelia strictissima*, each carrying large pollen loads, and two were collected on *Thelesperma megapotanicum*, but carried less than ten pollen grains. Thus, we do not yet know what the females of this species are doing at Monahans. Finally, three females of *Augochloropsis sumptuosa* were collected with heavy pollen loads, two on *Argemone gemone polyanthemos* and one on *Mentzelia strictissima*. All of these bees were collected between sunrise and 10:00 A.M.

Other bees and wasps (Hymenoptera)

We collected bees in a diversity of families, including Andrenidae, Anthophoridae, Apidae, and Megachilidae, most often on plants other than Onagraceae. *Martinapis enteicornis* (family Anthophoridae) was collected exclusively on *Gaura coccinea*, but carried little pollen (Table 6). A single *Diadasia rinconis* (Anthophoridae) male carried *Calylophus berlandieri* pollen (Table 5), whereas 11 females and 20 males were collected on *Argemone polyanthemos*, all but one female laden with pollen (Table 10). These female *D. rinconis* were observed to be sleeping inside the poppies shortly after sunrise. A single female of *Centris caesalpiniae* (Anthophoridae) was collected on *Calylophus berlandieri*, carrying a heavy load of pollen (Table 5). A single *Bombus pennsylvanicus* (Apidae) worker was collected on *C. berlandieri* (Table 5), but ten were encountered on *Mentzelia strictissima* (Table 9), all carrying large pollen loads of the plants visited, and mostly collected between sunrise and 10:00 A.M. All are putatively reliable pollinators of the plants visited, though their densities are low in this ecosystem. *Apis mellifera* (Apidae) was a common pollen forager on *Calylophus hartwegii* for several hours after anthesis at a degraded site in Brewster County (site 2), but not at Monahans Sandhills (site 9), and the honeybee workers were not observed to make contact with the stigmas while collecting pollen. They were not observed attempting to collect nectar, which normally is quickly harvested by sphinx moths (*Hyles lineata*) that appear just at the time of anthesis.

Five species of wasps, each in a different family (Ichneumonidae, Scoliidae, Sphecidae, Tiphiidae, and Vespidae) were collected on *Thelasperma megapotamicum* at the Monahans Sandhills (site 9) in western Texas. Almost all of these wasps (8 out of 9) carried major pollen loads (> 50 grains), so individually all except the undetermined ichneumonid wasp appear to be effective pollinators, albeit at low densities in the population.

Beeflies (Diptera)

Ten species of Bombyliidae were flower visitors at our study sites, belonging to at least six genera. Many beeflies visit *Calylophus berlandieri*, mostly carrying small to moderate (< 100 grains) pollen loads (Table 5); many of the numerous beeflies on *Thelesperma* carry somewhat larger pollen loads

(Table 8). These two plant species account for most beefly visitation in our analysis, but all plant species except *Calylophus hartwegii* had at least one beefly visitor. Beeflies tend to be most active in the hot midday period and are very hard to catch, even with a running start with the sweep net. We unintentionally baited individuals of *Poecilanthrax effrenus* at two separate populations of *Calylophus berlandieri* at site 9 (Table 1). Although the beeflies apparently were attracted to onagrad floral chemicals on clothing and nets, we assigned them to either *C. berlandieri* or *Thelesperma* depending on each individual's pollen load.

Two additional species of beeflies, *Heterostylum robustum* and *Poecilognathus scolopax* (Bombyliidae), also visited flowers of *Calylophus berlandieri* (Table 5). We observed *H. robustum*, a hirsute, golden-colored beefly that hovered over the flowers collecting nectar only at midday; most specimens carried heavy pollen loads. On the other hand, *Poecilognathus scolopax*, a cream-colored and less hairy beefly than *Heterostylum*, foraged mostly in early morning, landing on the flower and pushing about halfway into the floral tube, presumably to reach the nectar. Despite the scarcity of hairs and their nectar-gathering habits, most individuals of *P. scolopax* carried some *Calylophus* pollen, though only one carried more than 100 grains (Table 5). Both species are effective pollinators, since many individuals actively forage among plants and contact stamens and stigmas during flower visits.

Poecilanthrax effrenus (Bombyliidae) is a medium-sized, orange and black beefly that divided its time between the onagrad *Calylophus berlandieri* (Table 5) and the composite *Thelesperma* (Table 8) during the warmest parts of the day. In fact, of all the beeflies in this analysis collected with pollen loads, 76 of 78 individuals (97%) visited one of these two plant taxa; only one individual of *Poecilognathus scolopax* was collected each on *Mentzelia* (Table 9) and *Argemone* (Table 10). In conclusion, it appears that the beeflies of the Monahans Sandhills are either onagrad foraging specialists or composite foraging specialists, or in the case of one species, generalized enough to visit onagrads, composites, and other taxa.

Beetles (Coleoptera)

Like beeflies, flower-visiting beetles were most abundant in the hottest parts of the day, although we collected some beetles at other times. They are most significant as floral visitors of *Calylophus berlandieri* (80 individuals of 10 species, 60 of which carry some pollen; Table 5), where they ate pollen and other flower parts and regularly contacted the stigmas. They also fly between plants and are probably effective pollinators. The beetles *Altica* sp. indet. (Chrysomelidae) and *Achmaeodera mixta* (Buprestidae) together accounted for 25% (63 of 252) of all insects collected on flowers of *C. berlandieri*, but carried less than 8% of the cumulative pollen load (Table 5). At least some beetles were collected on all plant species in our data set, and in all three non-Onagraceae species (Tables 8–10), at least one beetle carried a large pollen load. However, beetles did not cumulatively constitute a major class of flower visitors or of pollen carriers for any plant species other than *C. berlandieri*. Primack and Silander (1975) reported beetles as effective pollinators of the day-flowering *Oenothera fruticosa* L. (Onagraceae) in North Carolina, although they were secondary in importance to introduced honeybees as pollinators. We did not observe beetle larvae feeding on any plants at our study site.

Moths and butterflies (Lepidoptera)

Butterflies were rare at the Monahans Sandhills site in western Texas in 1999 and 2000, possibly due to prolonged drought conditions. Scattered individuals of five butterfly families visited plants in our study communities, but in only two instances were they carrying any pollen. Three individuals of *Euptoita claudia* (Nymphalidae) carried small amounts of *Thelesperma* pollen, and a single male sachem skipper (*Atalopedes campestris huron*; Hesperiidae) carried a major load (> 50 grains) of *Mentzelia* pollen, each of them foraging during the noon to 4 P.M. period.

Moths, on the other hand, were the most common group of insects in our analysis. Four families of moths (Geometridae, Noctuidae, Pyralidae, and Sphingidae) are represented in this data set, and all limited their flower visitations to species of Onagraceae, although a few carried pollinia of an unknown and unseen species of *Asclepias* (Apocynaceae, Asclepiadoideae) on the tips of their legs. Even though these four moth families account collectively for 622 of the 1299 total insects collected (48%), they generally carry small pollen loads; only 59 of these 622 individuals (9%) carry more than 50 pollen grains, our pollen-load threshold for major pollinators. This major discrepancy between the visitor frequency and pollen load in moths may be a collecting artifact (i.e., pollen is lost from moths in the capture process more easily than from other insects), but more likely has a structural explanation.

The pattern of pollen deposition on the bodies of

moths found during pollen load analysis differs from the pattern observed on most other insect visitors. On many insects, especially those that forage primarily for pollen rather than nectar, we found most or all pollen on the ventral surface of the body. Hymenoptera frequently carried massive pollen loads, concentrated in and around specific pollen-gathering structures such as corbiculae or scopae. Most individuals of Coleoptera, Diptera, and Neuroptera also carry most or all of their pollen loads on their ventral surfaces. Some pollen grains also were found on the head and around the mouthparts of many insect visitors. However, in all groups of moths in our sample except the Sphingidae, most or all of the pollen was found on the proboscis, with relatively less on the ventral thorax, abdomen, and legs. This is true even on freshly collected specimens handled carefully to avoid pollen loss. This relative absence of pollen on the ventral surfaces of moths may be due to a general lack of hairs and other epidermal features that might trap pollen on those body parts, and also to the presence of scales on Lepidoptera, which may impede pollen adherence. It is unclear whether pollen on the moth proboscises effects pollination as well as that on the ventral surfaces, but we recorded total pollen present (proboscis and ventral body) for all lepidopteran visitors.

For the non-sphingid moths in our sample, most of the pollen load (ca. 85%) adheres to the proboscis, with much smaller amounts on the legs (less than 10%) and ventral thorax and abdomen (less than 5%). We observed a similar distribution of pollen on museum specimens of noctuids and geometrids examined at the Field Museum. Because most moths land on the staminal filaments while extending their proboscises to gather nectar, with the ventral thorax and abdomen pressed against the anthers and stigma, this lack of ventral pollen is puzzling. If pollen falls off or even is "dusted" off during handling of the specimens, one might expect comparable pollen loss on other types of insects, and perhaps similar loss of pollen from moth proboscises, but this is not observed. Ventral deposition of pollen on moths surely must occur, but perhaps adherence of pollen to moth scales is weak, at least relative to adherence on insects with hairy or scabrous ventral surfaces. If so, the pollen loads counted for moths in our analysis may underestimate the actual pollen carried by the moths, and underestimate their efficacy as pollinators. A comparative experimental analysis of pollen adherence to insect bodies would be necessary to resolve this question, and would be very useful for determination of pollinator effectiveness.

Sphingidae

Commencing at twilight, there is a surge in activity of the sphingid moth *Hyles lineata* on flowers of *Calylophus hartwegii,* and to a lesser degree, *Oenothera rhombipetala.* Difficult light conditions and the speed with which these moths move made catching them a particular challenge. Like other moths, Sphingidae carry pollen on the proboscis, but unlike other moths, they also carry substantial pollen on their ventral surfaces. Nonnenmacher (1999) observed ventral pollen deposition on sphingid moths visiting *Oenothera macrocarpa* (Onagraceae) on the Konza Prairie (Riley Co., Kansas, U.S.A.). This species is rather similar in floral morphology to *Calylophus hartwegii,* and elicits similar behavior by the sphingid moth visitors.

Geometridae

Whereas large sphingid moths forage on onagrad taxa with long corolla tubes at twilight, small geometrid moths (as well as somewhat larger noctuids and pyralids) actively visit freshly opened flowers of *Gaura coccinea.* Gregory collected moths on this species from 7:00 P.M. until midnight, in both the Monahans (sites 4 and 8; Table 1) and the Transpecos (sites 1 and 6) in western Texas. In both cases, small moths were most abundant until about 9:30 P.M., after which larger noctuids predominated. Most of the geometrid moths are an undetermined species of *Semiothisa,* which accounts for 47 of 238 insects (20%) caught on *G. coccinea* flowers. Even though most carry small pollen loads, they may be effective pollinators of *G. coccinea* as they fly among plants and land on flowers to forage nectar.

Noctuidae

Raven and Gregory (1972a; also Raven, 1979) suggested that noctuid moths are the primary pollinators of most species of *Gaura,* and our data support this contention at least in part. The most numerous pollinators of *G. coccinea* are four species of noctuid moths and one geometrid; of the nine major pollinators of *G. villosa,* two species of noctuid moths, *Bulia deducta* and *Melipotis indomita,* account for 53% of total visitors but less than 10% of the total pollen load (the other major pollinators are antlions and bees; Table 11). If, as we discussed above, the small pollen loads on these noctuid taxa are an artifact of collecting and/or curating moth specimens, then the importance of noctuid moths as pollinators of these *Gaura* species may be underestimated in our analysis. However, even if noctuid moths carry only small pollen loads, the sheer

number of these insects actively moving that pollen among plants clearly marks them as important and effective pollinators.

Bulia deducta and *Melipotis indomita* (Noctuidae, subfamily Catocalinae) were active throughout the night, with an activity peak between 10:00 P.M. and 2:00 A.M. Both of these species exhibited interesting behaviors. At site 9 in Aug. 1999, individuals of *M. indomita* came to the vicinity of *Oenothera rhombipetala* plants an hour before sundown when the flowers open and alighted on the sandy ground, where they were perfectly camouflaged. This behavior enabled them to visit the flowers as soon as they burst abruptly into bloom at twilight, in competition with a dramatic influx of sphingid moths. It may in fact be essential for *Melipotis* to forage at newly opened flowers before the larger sphingid moths, with their longer proboscises, take too much nectar from the long floral tubes of the *Oenothera* (20–30 mm; Munz, 1965). *Melipotis* also co-foraged with sphingids during the twilight anthesis period in Brewster County (site 2 in May 2000) on *Calylophus hartwegii*, which also has relatively long floral tubes (19.2 mm; Table 3), but we were unable to observe if they clustered around plants prior to anthesis. We did not observe either clustering or co-foraging behavior in *M. indomita* when it visited flowers of either species of *Gaura* (floral tubes 2.4–5 mm long; Table 3), which are seldom visited by sphingid moths.

Bulia deducta exhibited two foraging strategies on *Gaura villosa*. Commonly, this noctuid moth alighted upon the staminal filaments and style, and rested its wings while feeding on nectar. On several occasions, however, a moth would land on the floral tube and ovary, below the petals and stamens, and reach its proboscis between the petals and into the floral tube without contacting the stamens or stigma and therefore not effecting pollination. This behavior was observed at site 9 in May 2000, when one of the largest antlions, *Paranthaclisis hageni*, was present. In May 2001, this antlion species was particularly abundant in the large population of *G. villosa* at Monahans Sandhills (site 9), and no moths were present, a most unusual situation for this system. Abundant moth scales on the bodies of these antlions suggest they may be preying on moths at the same time as they forage for nectar.

Pyralidae

The garden webworm (*Achrya rantalis*) was the primary pyralid moth encountered. This species, collected on *Gaura villosa* both after midnight (2:30–4:30 A.M.) and before sunrise (5:30–7:00 A.M.), carried hardly any pollen. Like several of the smaller noctuid moths, these pyralid moths were shorter than the length of the stamen filaments. Thus, they could land near the throat of the floral tube and touch neither the anthers nor the stigmas. These infrequent visitors may be nectar robbers, but in any event are not effective pollinators.

Antlions (Neuroptera)

The first antlion of this study was recovered taking nectar from a population of *Gaura villosa* just south of the Kiowa National Grassland (Carrizo Creek patch, Union County, New Mexico, 23 July 1999, 2:00–4:00 A.M.). This female *Scotoleon minusculus* (Neuroptera, Myrmeliontidae) carried about 20 pollen grains of *Gaura* on its legs and ventral surfaces. Insofar as we know, this specimen appears to provide the first unambiguous documentation of pollen transport and pollination by any member of family Myrmeleontidae. There are several reports in the literature of floral visitation (nectar and pollen foraging without clear pollination) involving other Neuroptera, especially *Sialis* (alderfly) and *Hemerobius* (brown lacewing) on Apiaceae (Müller, 1883; Proctor & Yeo, 1973; Proctor et al., 1996), but in no cases are they reported as anything other than rare and minor floral visitors. Müller (1883) reported that only 13 of 5231 (0.2%) pollinator visits he observed involved Neuroptera, and many of those involved *Panorpa*, now considered in the order Mecoptera (scorpionflies). This study provides clear evidence that antlions are major pollinators of *Gaura villosa*.

Additional specimens of *Scotoleon minusculus* (both males and females) were collected at site 9 in the Monahans Sandhills on *Gaura villosa* flowers in Aug.–Sep. 1999. Seven specimens were recovered from 5:30 to 7:00 A.M., while it was still dark, and observed to hover over and land on the flowers. All seven carried *Gaura* pollen, and four had more than 100 grains, mostly on the face, legs, and ventral thorax, with a few on the wings (Fig. 3). Six more antlions were collected from 2:30 to 4:30 A.M., with five carrying more than 100 grains and two up to 1000 grains. Among this late-night sample was a male of *Vella fallax*, the largest antlion (60 mm long) in North America. This large antlion, carrying fewer than 10 *Gaura* pollen grains but well-dusted with moth scales, was observed on a flower in contact with stamens and stigma, suggesting that it may be an effective pollinator, but also that it may prey on moths. The specimen also exuded several droplets of clear liquid (nectar?) from the mouth during the pinning process.

Figure 3. Female adult antlion, *Scotoleon minusculus*, showing pollen of *Gaura villosa* on ventral surface of thorax; collected at Monahans Sandhills, Ward Co., Texas (site 9, Table 1); 1 Sep. 1999 (photo by R. Keating).

During a later trip to Monahans (site 9) in May 2000, we captured more individuals of *Scotoleon minusculus* on *Gaura villosa*, as well as specimens of three additional species of antlions, and were able to observe their foraging behavior more carefully. Most antlions were captured after midnight, when their clear wings and slender black bodies rendered them almost invisible. Typically, *S. minusculus* and *Brachynemurus hubbardi* spent long periods hovering around the plants, at a distance of up to one meter, approaching a flower and then suddenly withdrawing backward in a straight or elliptical pattern, but always facing the *Gaura* plant. The antlions landed on the *Gaura* flower much like noctuid moths, by grasping the filaments and style with their legs and crawling up the filaments until they could bury their faces in the throat of the floral tube. They sometimes remained in this position for several minutes. In this process, the ventral surface of the insect became covered with pollen, which was absent only from the posterior half of the abdomen on the most pollen-laden specimens. We observed as many as six individual antlions around a single plant, approaching and retreating before finally landing on a flower.

A possible reason for this apparent reluctance by the antlions to land became clear when we found and collected an antlion on a *Gaura* flower in the clutches of an unidentified white crab spider (fam. Thomisidae). We observed crab spiders on several occasions hiding beneath the petals and ambushing insects that landed on the flower, which is a typical and well-documented behavior for this family of spiders. We collected an additional crab spider and observed one additional antlion capture by a spider at site 9 on 20–21 May 2000 in the course of collecting 26 antlions. This suggests that predation of antlions (and other pollinators) by crab spiders is not an isolated occurrence in these communities, and may influence the foraging behavior of the antlions. Our observations also suggest that nectar foraging is important enough to antlions to risk possible predation during flower visitation.

Paranthaclisis hageni, the most abundant of the three large (> 40 mm in length) antlion species, also forages for nectar and lands on the *Gaura* flow-

ers just as do the smaller antlions. However, individuals of *P. hageni* are so heavy that they bend the entire inflorescence downward when they land. This antlion also is less likely to carry *Gaura* pollen and when it does, the pollen load is smaller (Table 4).

2. Analysis of Mixed Pollen Loads

Mixed pollen loads are relatively rare in this analysis, at least compared to other similar recent studies (Clinebell, 1998; Clinebell & Bernhardt, 1998; Nonnenmacher, 1999). This is despite the fact that all of the taxa studied here commonly occurred together in mixed species stands, with metapopulations of each plant species usually 50 to 1000 individuals. Here we discuss these mixed loads by shared plant species pairs.

Calylophus-Gaura *pollen loads*

The only insect visitors carrying these mixed loads were females of *Sphecodogastra danforthi*. We collected this species on both *Gaura villosa* and *Calylophus berlandieri* at the Monahans Sandhills (site 9) in August 1999, May 2000, and May 2001. Of the 94 females collected with pollen on *Calylophus*, 13 carried *Gaura* pollen, of which 12 carried more than 50 *Gaura* grains out of 200 total grains counted, or > 25% (Table 5). Of the 20 females collected on *Gaura*, one carried about equal amounts of *Calylophus* and *Gaura* pollen (Table 4). The grains of *C. berlandieri* are smaller, with prominent basal constrictions of the apertural protrusions (see Praglowski et al., 1988, fig. 1G), compared with the larger grains of *G. villosa* (Praglowski et al., 1988, fig. 2F).

Little pollen of any other plant was recovered on other individuals of *Sphecodogastra danforthi*, indicating that this bee is a strong oligolege for Onagraceae (McGinley, 2003). Morning sampling of both onagrads was roughly equal, suggesting that these halictids prefer *Calylophus* over *Gaura*; this is supported by the fact that we observed the bees foraging for nectar on the *Calylophus*, whose flowers open in the morning. By contrast, *Gaura villosa* opens in the evening and its nectar is collected all night long by moths and antlions.

Calylophus-Thelesperma *pollen loads*

Two species of beeflies at Monahans (site 9) carried this particular mixed pollen load. Eight of 25 individuals (32%) of *Poecilanthrax* collected on *C. berlandieri* carried such mixed loads, as did two of three *Exoprosopa* sp. 1. Flowers of *C. berlandieri* and *Thelesperma* are borne at about 20–30 dm height, much lower than those of other co-blooming taxa except for *Gaura coccinea*, which does not occur in the immediate vicinity of most populations of these two plants. By contrast, flowers of *Gaura villosa*, *Mentzelia*, and *Argemone* are borne at about 60–120 dm height. This suggests that the beeflies may prefer to forage among shorter vegetation at Monahans.

Other mixed pollen loads

The only other mixed load encountered on more than two individuals of any insect species was a mixed pollen load of *Gaura coccinea* and *Dalea* sp. indet., found on five of six male anthophorid bees (*Martinapis enteicornis*) collected on *G. coccinea* at site 5 in the Monahans region. Again, these flowers are held at a height of about 20–30 dm, and may represent a foraging height preference.

The very low relative abundance of mixed pollen loads in this large sample of insect visitors was unexpected and surprising. A possible explanation may derive from the fact that the data set is so heavily loaded with onagrad oligoleges—namely, all the antlions, most of the moths and bees (especially in *Sphecodogastra* and *Erylaeus*), and some beeflies. This paucity of mixed pollen loads is in spite of careful examination of pollen wash slides for virtually every individual insect for which a potential for a mixed load existed.

Conclusions

Our primary study site at the Monahans Sandhills in western Texas represents a fairly simple plant community that supports a diversity of insect pollen and nectar foragers. Because this is a hot semi-desert community, many insects avoid the heat of the day by foraging from early evening to early morning, with only a few insect groups active between 10:00 A.M. and 5:00 P.M. Several plant species experience intense and predictable periods of visitation by specific insects, usually coinciding with the onset of anthesis. An obvious conclusion of this study is that floral visitation—and effective pollination—can take place throughout the diurnal cycle, and that some visitors are active only during the night. Another conclusion is that although each plant species has one or a few predominant pollen carrier(s), all species have a diversity of major pollen carriers (> 50 grains), including more than one order of insects in all species except *Gaura coccinea*.

Tables 11 and 12 indicate that the major pollen carriers (all insects carrying more than 50 pollen

grains of the plant species in question) in the Monahans ecosystem are largely non-overlapping among the seven primary plant species we studied. In part, this may reflect the floral morphology and time of flowering in the species of Onagraceae. In the night-blooming species, those with shorter (1.5–11 mm) corolla tubes (*Gaura* spp.) attract mostly noctuid moths (Raven & Gregory, 1972a) and, in the surprising case of *G. villosa*, antlions, whereas onagrads with longer (16–50 mm) floral tubes (*Calylophus hartwegii*) attract more sphingid moths (Towner, 1977). The day-flowering *C. berlandieri* attracts day-flying bees and other insects, but not moths. Even in the day-flowering non-onagrad species, there also is little overlap among pollen carriers. Few comparable studies that examine floral visitation rates and pollen load through diurnal and seasonal cycles are available, so it remains to be seen if this high degree of pollinator specificity is the exception or the rule. This report is the first in a series of analyses of North American plant communities that include *Gaura*, *Calylophus*, and other species of Onagraceae, in which we intend to examine the evolution of pollination biology in this group, and to compare the community pollination biology of these different assemblages of taxa.

Even with our relatively large sample sizes, some members of the community pollinator guild remain rare in our data set. This is particularly true for the largest species in various insect groups, where we collected only single specimens of two large antlions, an underwing noctuid moth, a beefly, an anthophorid bee, and a *Euphoria* flower beetle, each the largest taxon in their group. This may simply indicate that these large pollinators are less common, but it also suggests that our description of this guild may be incomplete.

An apparently unavoidable cost in the census of these rare pollinating species is the collection of large numbers of the commoner species in the community. However, understanding the biology and behavior of these rare taxa and the role(s) they play in natural communities may be critical to understanding those communities. Some of the taxa that are rare in our analysis may be more common at other times, for example, when the communities are not experiencing drought conditions. Pettersson (1991) found strong year-to-year variation in the abundance of pollinating moths on *Silene vulgaris* in Sweden. We suggest that sustained and detailed studies that include a moderate amount of repeated collecting over several years are essential to elucidating the roles of rare species.

In terms of community pollination ecology in western North America, our results prompt two observations: (1) Analysis of pollination guilds is obscured when a study area is overwhelmed by large populations of the European honeybee, *Apis mellifera* (see also Primack & Silander, 1975). The general scarcity of honeybees in our primary study site in the sandhills of Ward Co., Texas (site 9), demonstrates that the site is relatively pristine, with its native pollination guild intact. At our site in Brewster Co. (site 2), however, the invasive honeybee appears as a major pollen carrier of *Calylophus hartwegii*, a species with apparent specializations for hawkmoth pollination. (2) Disturbed and degraded assemblages of plant species may give a similarly distorted picture of the pollination guild, compared with an undisturbed site. Our analysis of this relatively intact community shows both a high degree of pollinator specialization and the presence of a diversity of relatively rare insect visitors as pollinators.

The richness of the data that can be harvested when studies in pollination ecology span a variety of co-blooming dominant plants in different plant families is much more interesting, it appears to us, than studies that focus on a single species, genus, or family (see also Clinebell, 1998, 2004). Such community-level studies give an overview of the role a given insect species plays in the overall dynamic of the community, and the degree of fidelity enjoyed by a given plant species in the ecosystem. These comparisons allow the use of statistical analysis and thus elevate studies of pollination biology from the status of descriptive natural history into the realm of hypothesis-driven quantitative ecology, as well as the identification of probable coevolutionary relationships between plants and insects.

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A SYSTEMATIC OVERVIEW OF FRANKENIACEAE AND TAMARICACEAE FROM NUCLEAR rDNA AND PLASTID SEQUENCE DATA[1]

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ABSTRACT

Within the sister families Frankeniaceae and Tamaricaceae (order Caryophyllales) we investigate the systematic placement of *Hypericopsis*, *Myrtama*, and *Hololachna*, which have at times been lumped into other genera (*Frankenia*, *Tamarix* or *Myricaria*, and *Reaumuria*, respectively) or, alternatively, retained as small distinct genera. We describe their previous taxonomic placements and analyze sequence data from the nuclear ribosomal region 18S and chloroplast regions *rbc*L and tRNA Ser (GCU)/ tRNA Gly (UCC) intergenic spacer for the genera in both families, finding cladistic support for the placement of *Hypericopsis* within *Frankenia*, and for *Myrtama* and *Hololachna* as distinct genera.

Key words: 18S, *Frankenia*, Frankeniaceae, *Hololachna*, *Hypericopsis*, molecular systematics, *Myricaria*, *Myrtama*, *rbc*L, *Reaumuria*, Tamaricaceae, *Tamaricaria*, *Tamarix*, tRNA Ser (GCU)/ tRNA Gly (UCC) intergenic spacer.

The plant families Frankeniaceae and Tamaricaceae consist of halophytic and xerophytic shrubs and trees, and occasional herbaceous plants. They have historically been placed as sister families because they share characters such as secondary chemistry, gland structure, and often petaline scales (*Frankenia* L., *Hololachna* Ehrenb., and *Reaumuria* L.). As a group they have, until lately, been in the order Violales (e.g., Cronquist, 1988; Thorne, 1992) due to their polypetalous flowers and mostly parietal placentation. Recent molecular analyses (sensu APG, 1998) have moved both families to the Caryophyllales, close to such families as Droseraceae, Plumbaginaceae, and Polygonaceae (e.g., Lledó et al., 1998; Soltis et al., 2000; Cuénoud et al., 2002), which are caryophyllid families that share a straight embryo and endosperm (Spichiger & Savolainen, 1997).

The two families Frankeniaceae and Tamaricaceae have obvious morphological differences in phyllotaxis (opposite in Frankeniaceae, spiral in Tamaricaceae) and leaf shape (strongly revolute to almost flattened in Frankeniaceae, flattened or subulate in Tamaricaceae). Molecular studies, such as those mentioned above, were not focused on intrafamilial relationships, and thus included only one species from Frankeniaceae and/or Tamaricaceae. This is the first molecular systematic investigation within Frankeniaceae, and the first such investigation in Tamaricaceae using multiple independent loci. Zhang et al. (2000) have previously analyzed the internal transcribed spacer region (ITS) and intervening 5.8S subunit of the 18S–26S nuclear ribosomal DNA for various Tamaricaceae.

The Frankeniaceae currently contain one genus, *Frankenia*, which encompasses the monotypic *Hypericopsis* Boiss. [= *Frankenia persica* (Boiss.) Jaub. & Spach]. Tamaricaceae presently have three larger genera (> 10 species), *Tamarix* L., *Myricaria* Desv., and *Reaumuria*, and two smaller genera (1 to 2

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species), *Myrtama* Ovcz. & Kinzik. and *Hololachna*. Here we discuss the taxonomic history of the smaller genera, and present nuclear and chloroplast sequence data analyses in an effort to clarify their phylogenetic placement.

Frankeniaceae

Frankenia contains about 70 to 80 species (Mabberly, 1993; Kubitzki, 2003) distributed in many temperate and subtropical regions on saline or gypseous soils. *Frankenia persica*, a narrow endemic from Iran, is found mostly on the salty shoreline soils of lakes near Shiraz, between 1300 and 1700 m elevation. This species was originally described as the monotypic genus *Hypericopsis* containing *H. persica* (Boissier, 1845), with 5 to 6 calyx lobes and 6 to 7 petals, compared to the usual 5-lobed calyx and 5 petals in *Frankenia*, but note that there are more recently described *Frankenia* species with 5 to 6 calyx lobes (e.g., *F. punctata* Turcz.) or 4 to 6 petals (e.g., *F. interiosis* Ostenf.). Soon after Boissier's original description Jaubert and Spach (1847) moved *H. persica* into *Frankenia*, an action that was not universally adapted, as the name *H. persica* is still often applied (e.g., Chrtek, 1972; Kubitzki, 2003). According to Niedenzu (1925a), *F. persica* and the rest of *Frankenia* differ mainly in stamen number (16 to 24 vs. 3 to 12, respectively) and petal size (8–12 vs. 5–7 mm), though when considered worldwide, there are *Frankenia* with petals up to 16 mm (e.g., *F. cordata* J. Black).

Tamaricaceae

Tamaricaceae contain about 80 species (Mabberly, 1993) found in temperate and subtropical Africa and Eurasia on salty or dry areas of deserts, steppes, sandy shores, and along rivers (Gaskin, 2003). *Tamarix* is the largest genus in the family, containing approximately 54 species (Baum, 1978) that naturally occur in northern Africa and Eurasia. There are also two disjunct species, *T. angolensis* Nied. (Angola, Namibia, and South Africa) and *T. usneoides* E. Mey. ex Bunge (Namibia and South Africa). Naturalized species, often severely invasive, are found in the U.S.A, Mexico (mostly *T. ramosissima* Ledeb. and *T. chinensis* Lour.) (Ríos & García, 1998; Gaskin & Schaal, 2002), and Australia (*T. aphylla* (L.) Karst.) (Griffin et al., 1989). *Myricaria* contains about 10 species of shrubs (some prostrate) ranging from Europe to mainly central Asia. The only consistent morphological difference between these two genera is that there are 10 monadelphous stamens in *Myricaria* versus 4 to 14 distinct stamens in *Tamarix*. *Myricaria* tends to have sessile, cushion-like stigmas (or at least no obvious style or style branches) and a stipitate seed pappus, while *Tamarix* tends to have a short stylodium and a sessile pappus, but there are exceptions (see Baum, 1978: 14).

Myricaria elegans Royle was originally described from the Kunawar region of the western Himalayas (Royle, 1835). This species, now accepted as *Myrtama elegans* (Royle) Ovcz. & Kinzik., has 10 stamens, flat leaves, and no obvious style, so its original placement in *Myricaria* was reasonable. However, the stamens are distinct (vs. monadelphous in *Myricaria*) and the pappus is sessile (vs. stipitate), which is presumably why Baum transferred *Myricaria elegans* to *Tamarix* in 1966, giving it the name *T. ladachensis* Baum (because the name *T. elegans* Spach was already occupied). In 1977 Ovczinnikov and Kinzikaeva considered the species as intermediate to *Myricaria* and *Tamarix* and placed it in its own genus, *Myrtama*. The next year, *Myricaria elegans* was transferred to another novel genus, *Tamaricaria* Qaiser & Ali (1978), nom. illegit. Zhang and Zhang (1984), Tang (1986), Liu (1995), and Xi (1988) further discussed the taxonomic status of *Myricaria elegans* citing different morphological evidence such as pollen and seed morphology and agreed with its original placement in *Myricaria*. Zhang et al. (2000) sequenced the nuclear ribosomal ITS region for various Tamaricaceae, and due to high levels of heterozygosity in *Myrtama*, proposed that it is either a recent hybrid of *Tamarix* and *Myricaria*, or a long established intermediate genus. Zhang (2001) investigated pollen morphology and supported placement in *Myrtama*.

Reaumuria is a genus of about 12 small shrub species ranging from Europe to central Asia and is easily distinguished from all other *Tamarix* and *Myricaria* by its solitary flower vs. clusters and the presence of lateral scales on the adaxial base of its petals. In 1827 Ehrenberg described the new monotypic genus *Hololachna*, containing a central Asian Tamaricaceae with solitary flowers (*Hololachna songarica* Ehrenb.). He placed it there instead of in *Reaumuria* because it had a unique 2- to 4-carpellate ovary, 2 to 4 subulate style branches, and 8 to 10 stamens, instead of the 5-carpellate ovary, usually 5 filiform style branches, and 5 to many stamens typical of *Reaumuria* (Ehrenberg, 1827: 273). *Hololachna* also has lateral scales on its petals like *Reaumuria* (Niedenzu, 1925b), though they are almost indistinct at 1 mm in length. In 1873 Hooker added *Hololachna shawiana* Hook. f. ex Henders. & Hume (not sequenced herein) to the genus (Henderson & Hume, 1873). Recent authors

(e.g., Schiman-Czeika, 1964; Mabberly, 1993; FCC, 2002; Gaskin, 2003) have treated *Hololachna* as part of *Reaumuria*.

Materials and Methods

We sequenced the tRNA Ser (GCU)/ tRNA Gly (UCC) intergenic spacer (IGS) (938 base pairs (bp) in Frankeniaceae and 765 bp in Tamaricaceae) and *rbc*L region (1325 bp) (both from the chloroplast genome), and the partial 18S region (971 bp) of the nuclear ribosomal DNA for selected Frankeniaceae and Tamaricaceae species. Phylogenetic analyses of the molecular data were used in an effort to clarify the taxonomic status of the smaller genera.

DNA Isolation, PCR Amplification, and Sequencing

Myrtama elegans, *Hololachna songarica*, *Frankenia* (7 species), *Tamarix* (5), *Myricaria* (3), and *Reaumuria* (4) were sequenced from fresh, silica-dried tissue. Vouchers (Appendix 1) are deposited at *Index Herbariorum* locations, or at the U.S. Department of Agriculture (*USDA*), Agriculture Research Service, Grassland, Soil and Water Research Laboratory, 808 E. Blackland Rd., Temple, Texas 76502-9601, U.S.A. (which is not listed in *Index Herbariorum*). All GenBank accessions AY099899 to AY099958 are new sequences obtained for this analysis. The sequences for *Frankenia pulverulenta* L., *Limonium arborescens* Kuntze, *Polygonum* sp. indet., and *Eriogonum flavum* Nutt. are from other studies (the citations can be found in GenBank <http://www.ncbi.nlm.nih.gov/Genbank>). There were no accessions of Polygonaceae species sequenced for both 18S and *rbc*L in GenBank, so we combined the 18S sequence of *Polygonum* sp. indet. with the *rbc*L sequence of *Eriogonum flavum*.

Genomic DNA was isolated using a modified CTAB method (Hillis et al., 1996). PCR amplification of the chloroplast intergenic region between tRNA-Ser (GCU) and tRNA-Gly (UCC) genes utilized the primer pair trnS (GCU) and trnG (UCC) of Hamilton (1999) with the following thermocycling conditions: 95°C initial denaturation (2 min.); 30 cycles of 95°C denaturation (1 min.), 55°C annealing (1 min.), 72°C extension (2 min.); and then 32°C termination (5 min.). Amplification of the *rbc*L plastid region utilized the primer pair *rbc*L5FOR (5′-gtcaccacaacagaaactaaagc-3′) and *rbc*L3REV (5′-gaattcaaatttgatctccttc-3′) (origin of primers unknown) with the cycling conditions varying only by an annealing temperature of 50°C. Amplification of the partial 18S region of the nuclear ribosomal DNA utilized the primer pair 18Sf (5′-gctaatacgtgcaacaaaccc-3′) and 18Sr (5′-ccttactatgtctggacctgg-3′) that we designed, also with an annealing temperature of 50°C. A 50-µl reaction was performed for each individual, and PCR products were purified by agarose gel electrophoresis followed by QIAquick Gel Extraction Kit. Purified PCR template was sequenced using the dideoxy chain termination method with ABI PRISM™ Dye Terminator Cycle Sequencing Ready Reaction Kit with AmpliTaq DNA polymerase. Specimens were electrophoresed in an ABI 373A automated sequencer following manufacturer's instructions. Sequences generated in this study are available on GenBank (see Appendix 1 for accession numbers).

Phylogenetic Analyses

Sequences were manually aligned using the software Se-Al (Rambaut, 1996). The sequence alignments are available upon request from the first author. Insertion/deletion events were treated as a fifth base. The tRNA Ser (GCU)/ tRNA Gly (UCC) IGS sequences were unalignable between the two families, so that data was used only for the intrafamilial analyses.

We tested for congruence of data sets with the partition homogeneity test in PAUP* version 4.0b3 (Swofford, 2000) (with 500 replicates), and it supports the null hypothesis that two data sets are congruent (congruence of 18S and *rbc*L data sets for interfamilial analysis: $P = 0.938$ (Fig. 1) as well as the congruence of 18S, *rbc*L, tRNA Ser (GCU)/ tRNA Gly (UCC) IGS data sets within either Tamaricaceae or Frankeniaceae: $P = 1$ (Fig. 2)).

Parsimony analyses of the data sets were performed using PAUP*. Branch and bound searches used tree bisection reconnection, collapse, and multrees options, with steepest descent not in effect. Ten runs of 10,000 replicate fast stepwise-addition bootstrap analyses were conducted to assess clade support, with the lowest consensus bootstrap score of those runs recorded. Templeton tests were performed by making alternate topologies in MacClade 4.0 (Maddison & Maddison, 2000), using these as constraints in PAUP* heuristic searches, then comparing the original and constrained topologies in the trees>tree scores>parsimony>nonparametric option of PAUP*. The range of resultant P values from the Wilcoxon's signed rank test (Rolhf & Sokal, 1995) was used to determine the statistical significance of the difference in length between the original and alternative topological hypotheses (significance at $P < 0.05$ in a one-tailed test). Pairwise distances (uncorrected "p" distances) for Tamarica-

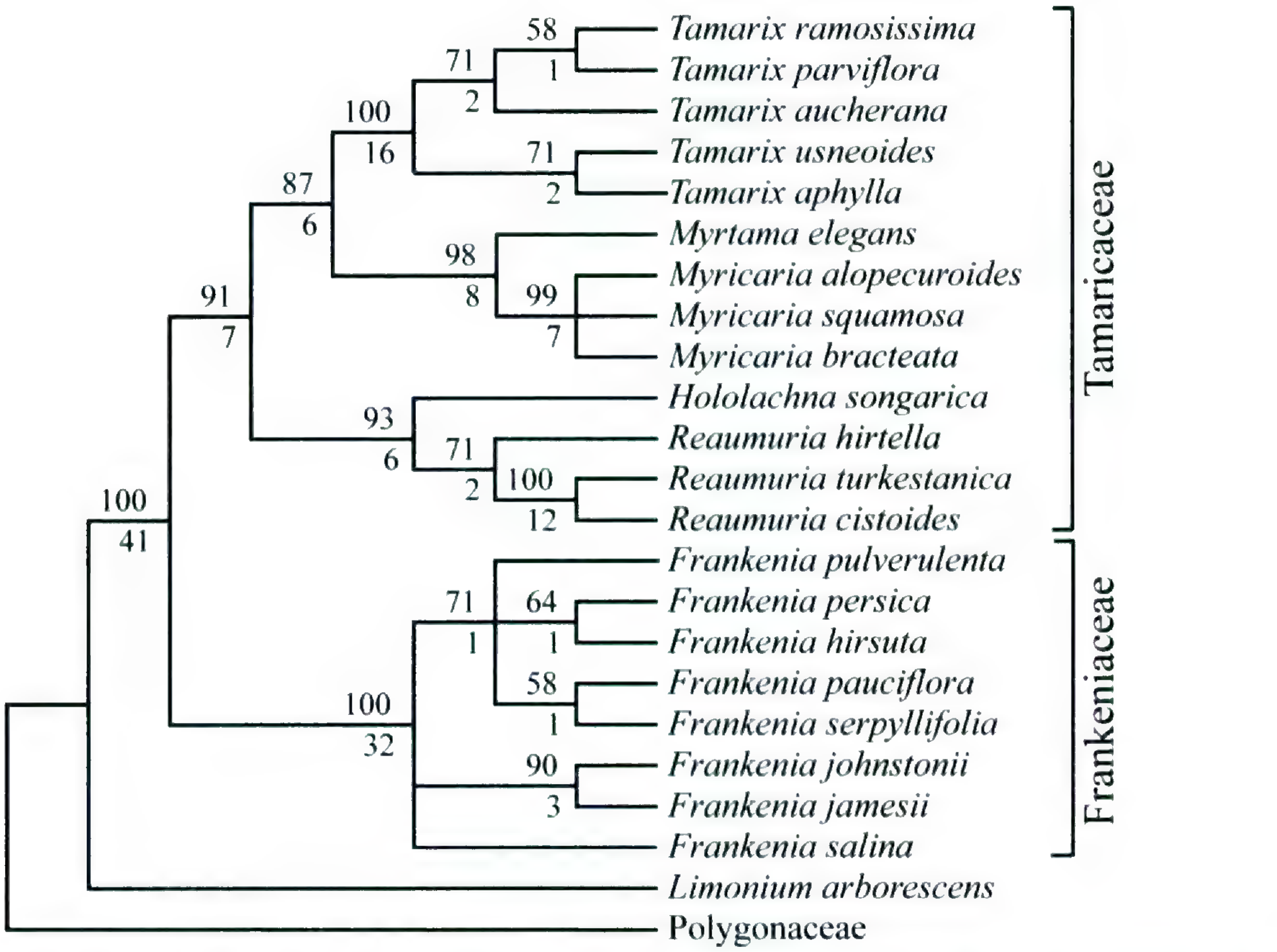

Figure 1. Interfamilial strict consensus cladogram of the four most parsimonious trees for the combined 18S (nrDNA) and *rbc*L (cpDNA) data set, 417 steps in length, RI = 0.895. With the uninformative characters excluded, CI = 0.719. Bootstrap percentages are above branches and decay values below. Polygonaceae are represented by a combination of 18S sequence from *Polygonum* sp. indet. and *rbc*L sequence from *Eriogonum flavum*.

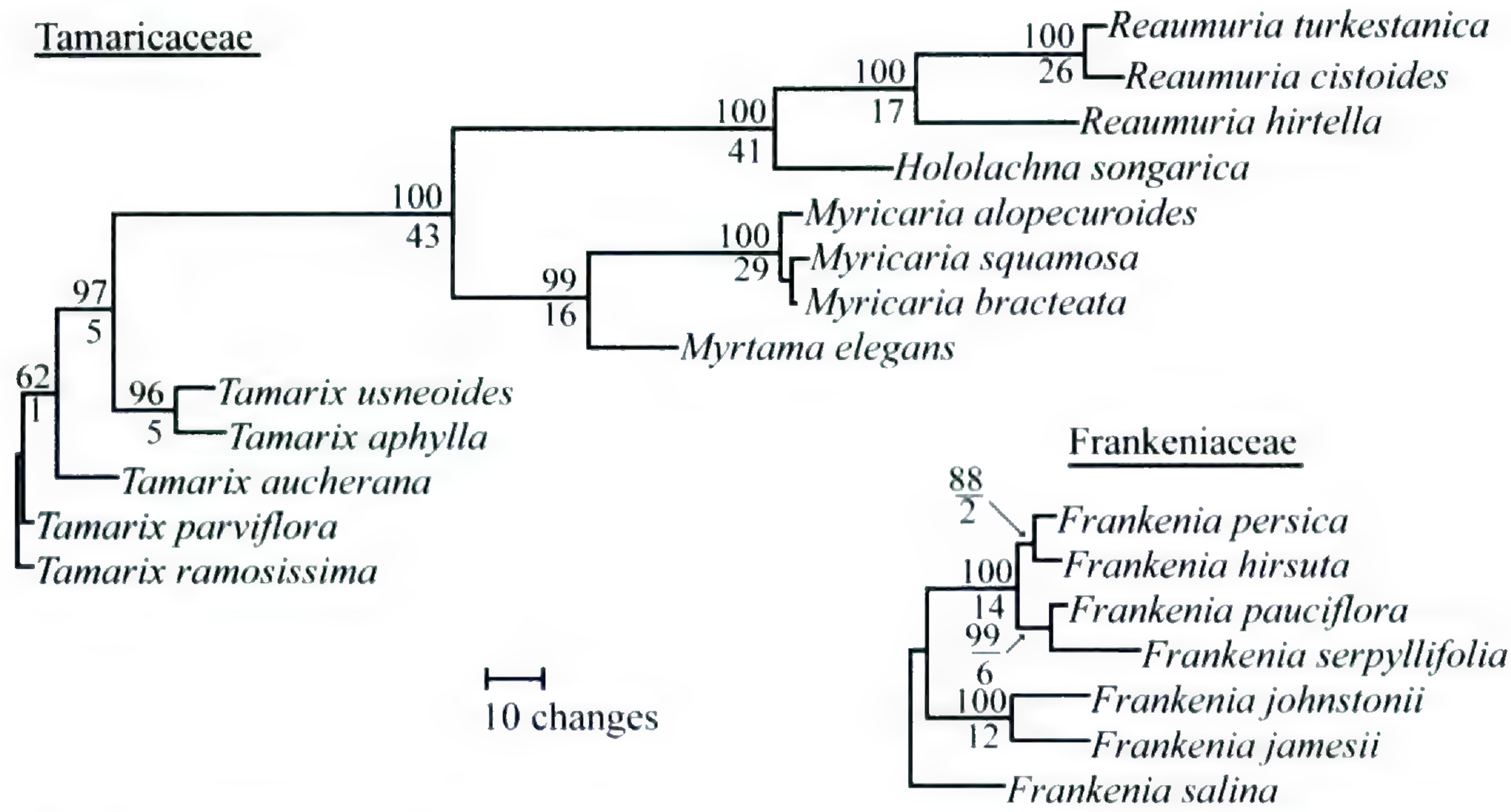

Figure 2. Intrafamilial phylograms for Tamaricaceae (above) and Frankeniaceae (below), from the combined 18S (nrDNA), *rbc*L (cpDNA), and tRNA Ser (GCU)/ tRNA Gly (UCC) IGS (cpDNA) data sets. Bootstrap percentages are above branches and decay values below. The Tamaricaceae diagram is the single most parsimonious tree, 372 steps in length, RI = 0.921. With uninformative characters excluded, CI = 0.798. The Frankeniaceae diagram is the single most parsimonious tree, 114 steps in length, RI = 0.912. With uninformative characters excluded, CI = 0.894.

ceae were calculated in PAUP*, and are listed in Appendix 2.

Results

FRANKENIACEAE AND TAMARICACEAE

The two combined 18S nrDNA and *rbc*L cpDNA data sets consist of 2296 aligned bases, of which 297 (12.9%) are variable and 172 (7.5%) are phylogenetically informative, with 80 (0.2%) of the data matrix cells scored as missing. Excluding the outgroups Plumbaginaceae and Polygonaceae, 187 (8.1%) sites are variable and 65 (2.8%) are potentially phylogenetically informative. The combined data set yields four most parsimonious trees (not shown) 417 steps in length (RI = 0.895). When the uninformative characters are excluded, CI = 0.719. The interfamilial consensus tree is presented in Figure 1. In a more rigorous test we searched for the shortest tree that could violate the constraint of a monophyletic Frankeniaceae. The best topology is 32 steps longer, and the null hypothesis of these two topologies being statistically similar is rejected ($P < 0.0001$ in a Templeton test).

Using only 18S and *rbc*L data, phylogenetic resolution is low within Frankeniaceae and Tamaricaceae. To improve this, we added data from the tRNA Ser (GCU)/ tRNA Gly (UCC) IGS. As this IGS region proved to be unalignable between families, we performed two separate intrafamilial analyses based on the 18S, *rbc*L, and tRNA Ser (GCU)/ tRNA Gly (UCC) IGS, one for each family. These trees are presented in Figure 2, and they are rooted to preserve the topology in Figure 1.

FRANKENIACEAE

The three combined 18S, *rbc*L, and the tRNA Ser (GCU)/ tRNA Gly (UCC) IGS data sets consist of 3234 aligned bases, of which 104 (3.2%) are variable and 40 (1.2%) are phylogenetically informative, with 15 (0.0%) of the data matrix cells scored as missing. The data sets yield a single most parsimonious tree 114 steps in length (RI = 0.912); with uninformative characters excluded, CI = 0.894. This intrafamilial tree shows strong support (bootstrap support (bs) = 100%) for *Frankenia persica* within the genus *Frankenia* (Fig. 2).

TAMARICACEAE

The three combined 18S, *rbc*L, and tRNA Ser (GCU)/ tRNA Gly (UCC) IGS data sets consisted of 3061 aligned bases, of which 277 (9.0%) are variable and 217 (7.1%) are phylogenetically informative, with 122 (0.3%) of the data matrix cells scored as missing. The combined data sets yield a single most parsimonious tree 372 steps in length (RI = 0.921); with uninformative characters excluded, CI = 0.798. This intrafamilial tree, presented in Figure 2, shows strong support for *Tamarix* and *Myricaria* as distinct, monophyletic genera (bs = 100%, $P < 0.0001$ in Templeton tests for both genera). *Reaumuria* is supported as monophyletic (bs = 100%, $P = 0.0007$ Templeton test) in the intrafamilial analysis (Fig. 2) with *Hololachna songarica* appearing as sister to this clade.

Discussion

FRANKENIACEAE AND TAMARICACEAE

The interfamilial consensus tree is presented in Figure 1. As was expected, Frankeniaceae and Tamaricaceae are each well supported in separate clades (100% and 91% bs, respectively, and $P < 0.0001$ in a Templeton test). The molecular analysis corroborates the earlier morphological data (such as secondary chemistry, gland structure, and often petaline scales) used as evidence of the close relationship of the two families. The four most parsimonious trees (not shown) for which we show the consensus in Figure 1 vary in the placement of *Frankenia pulverulenta* (which remains closest to or within the Asian and Australian Frankeniaceae species) and *F. salina* I. M. Johnst. (which remains closest to or within the American Frankeniaceae species), but neither case affects the following discussion.

Hypericopsis [= Frankenia persica]

Frankenia persica falls within the other *Frankenia* in the interfamilial analysis (Fig. 1). In the intrafamilial analysis, there is strong support for *F. persica* being in the Eurasian and Australian Frankenia clade (bootstrap = 100%), with the New World species forming a more distantly related group (Fig. 2). This clustering of Asian/Australian vs. American *Frankenia*, even though for a small set of taxa, is a useful corroboration of the molecular data sets. When we create an alternative topology in which *F. persica* is outside of the *Frankenia* clade in the interfamilial analysis, it is (barely) not statistically different in the rigorous Templeton test (P = 0.0588), but given the strong bootstrap support for inclusion of *F. persica* in the Eurasian and Australian *Frankenia* in the intrafamilial analysis (Fig. 2), we confirm *F. persica*, not *Hypericopsis persica*, as the proper cladistic designation for this species. The more numerous stamens (16 to 24 vs. 3 to 12) and larger petals (8 to 12 vs.

normally 5 to 7 mm) of *F. persica* appear to have been derived from an ancestral Eurasian *Frankenia* species.

Tamarix *and affined genera*

The intrafamilial data set shows strong support for *Tamarix* and *Myricaria* as distinct, monophyletic genera (Fig. 2). The three *Myricaria* species (Appendix 1) that we sampled are, as a clade, well supported as distinct from *Myrtama* (bs = 100%), and *Myrtama* is closer to *Myricaria* than *Tamarix* (pairwise distance from *Myrtama* to *Tamarix* is 0.023 to 0.026, while pairwise distance from *Myrtama* to *Myricaria* is 0.012 to 0.013; see Appendix 2). *Myricaria* species sequenced here are much closer to each other than they are to *Myrtama* (the greatest pairwise distance within the three *Myricaria* exemplars (0.002) is six times smaller than the pairwise distance between *Myrtama elegans* and the closest *Myricaria* (*M. bracteata*) (0.012); see Appendix 2). Zhang et al. (2000) originally found a high level of heterozygosity in the ITS nrDNA sequence of *Myrtama elegans* using DNA extracted from dried herbarium material. Here, we used fresh leaf material for DNA extraction and found no evidence of heterozygosity in our *Myrtama* nuclear sequence data, supporting the second hypothesis by Zhang et al. (2000) that *Myrtama* is an intermediate genus between *Tamarix* and *Myricaria*, and not a recent hybrid of the two genera. Given the current molecular data and the morphological intermediacy of *Myrtama* (10 stamens and sessile stigmas, as in *Myricaria*, but also the stamens are distinct and the seed pappus is sessile, as in *Tamarix*), we find support for *Myrtama* as a distinct genus. Others may wish to include *Myrtama* within a *Myricaria* sensu lato or a *Tamarix* sensu lato, but they should note that both molecular and morphological data would place *Myrtama* as the outlier of either group.

Reaumuria *and* Hololachna

Reaumuria is strongly supported (bs = 100%) as monophyletic in the intrafamilial analysis (Fig. 2) with *Hololachna songarica* appearing as sister to the rest of the genus. The greatest pairwise sequence variation (Appendix 2) between *R. cistoides*, *R. hirtella*, and *R. turkestanica* (0.017) is very similar to the smallest pairwise distance between *H. songarica* and any of our three *Reaumuria* (0.021). Given the morphological peculiarities of *H. songarica* compared to *Reaumuria* (2- to 4- vs. 5-carpellate ovary, 2 to 4 subulate vs. 5 filiform style branches, and 8 to 10 vs. 5 to many stamens) and our molecular placement of *H. songarica* outside of the clade containing three species of *Reaumuria*, we agree with Ehrenberg (1827) and Niedenzu (1925b) and consider *Hololachna* as a separate genus. Others may wish to include *Hololachna* within a *Reaumuria* sensu lato, but it should be noted that current molecular and morphological data would place *Hololachna* as the outlier of that group.

Conclusions

In our molecular analysis Frankeniaceae and Tamaricaceae are each monophyletic and retain their sister-family status as monophyletic taxa. This corroboration with earlier morphological data strengthens our phylogenetic understanding of the two families. In the past, *Frankenia persica*, *Myrtama elegans*, and *Hololachna songarica* have each been placed within their larger sister genera or alternatively each has been considered a separate genus, with morphological support for both cases. In Frankeniaceae we find strong molecular support for the inclusion of *F. persica* within *Frankenia*, confirming Frankeniaceae as a monotypic family. In Tamaricaceae we find strong molecular support for *Myrtama* being separate from *Myricaria* and *Tamarix*, as well as for *Hololachna* being separate from *Reaumuria*, though in both cases these taxa could also be considered outliers within each sister genus sensu lato.

Ongoing and future morphological and molecular research should lead us to a point of taxonomic stability within the two families. Of special interest are other Frankeniaceae genera such as *Anthobryum* Phil., *Beatsonia* Roxb., and *Niederleinia* Hieron., which, based on morphological data, are now considered to be within *Frankenia* (e.g., Whalen, 1987). These taxa were not available for molecular analysis, but we hope to test their current placement in future studies. Also, a molecular systematic analysis of *Frankenia* from Australia (where 46 of the approximately 70 to 80 species are found) is being undertaken by A. Craigie (Whalen lab, Flinders Univ., Adelaide, Australia).

Recent work in *Tamarix* includes molecular evidence of hybridization of phylogenetically diverse invasive species in the U.S.A. (Gaskin & Shafroth, in prep.) and a discussion of *Tamarix* biogeography (Zhang et al., 2003). Also, a more complete molecular phylogeny of *Tamarix* (Gaskin, unpublished data) is under way, including taxa from western Africa and southern Asia.

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Appendix 1. Collection vouchers and GenBank (⟨http://www.ncbi.nlm.nih.gov/Genbank⟩) accession numbers for taxa studied from Frankeniaceae, Tamaricaceae, and outgroup families Plumbaginaceae and Polygonaceae.

Species	Collection source, voucher and herbarium	GenBank acc. # 18S	GenBank acc. # *rbc*L	GenBank acc. # tRNA spacer
Frankenia hirsuta L.	Turkmenistan, *Gaskin 1065* (MO)	AY099947	AY099914	AY099954
Frankenia jamesii Torr. ex A. Gray	U.S.A. *J.L. Tracy 11(USDA)*	AY099951	AY099918	AY099958
Frankenia johnstonii Correll	U.S.A., *DeLoach s.n. (USDA)*	AY099949	AY099916	AY099956
Frankenia pauciflora DC.	Australia, *Whalen 99-3* (AD)	AY099946	AY099913	AY099953
Frankenia pulverulenta L.	GenBank	AF206914	Z97638	not used
Frankenia salina I. M. Johnst.	U.S.A., *Gaskin 75* (MO)	AY099950	AY099917	AY099957
Frankenia serpyllifolia Lindl.	Australia, *Whalen 00-6-3* (AD)	AY099948	AY099915	AY099955
Hypericopsis persica Boiss.	Iran, *Gaskin 955* (MO)	AY099945	AY099912	AY099952
Limonium arborescens Kuntze	GenBank	AF206953	AF206789	not used
Polygonum sp. indet.	GenBank	AF206996	not used	not used
Eriogonum flavum Nutt.	GenBank	not used	Z97648	not used
Hololachna songarica Ehrenb.	China, *DeLoach s.n. (USDA)*	AY099941	AY099908	AY099928
Myricaria alopecuroides Schrenk	China, *Wang Jian Feng 10 (USDA)*	AY099938	AY099905	AY099925
Myricaria bracteata Royle	Kazakstan, *Gaskin 1148* (MO)	AY099940	AY099907	AY099927
Myrtama elegans (Royle) Ovcz. & Kinzik.	China, *Al-Shehbaz 8433* (MO)	AY099937	AY099904	AY099924
Myricaria squamosa Desv.	China, *DeLoach s.n. (USDA)*	AY099939	AY099906	AY099926
Reaumuria cistoides Adam	Iran, *Gaskin 919* (MO)	AY099944	AY099911	AY099930
Reaumuria hirtella Jaub. & Spach	Israel, *Danin s.n.* (MO)	AY099942	AY099909	AY099931
Reamuria turkestancia Gorshck.	Turkmenistan, *Gaskin 1017* (MO)	AY099943	AY099910	AY099929
Tamarix aphylla (L.) H. Karst	U.S.A., *Gaskin 1223* (MO)	AY099936	AY099903	AY099923
Tamarix aucherana (Decne. ex Walp.) Baum	Iran, *Gaskin 771* (MO)	AY099933	AY099900	AY099920
Tamarix parviflora DC.	U.S.A., *DeLoach 00-04 (USDA)*	AY099934	AY099901	AY099921
Tamarix ramosissima Ledeb.	U.S.A., *Gaskin 97* (MO)	AY099932	AY099899	not used
Tamarix ramosissima Ledeb.	U.S.A., *Gaskin 103* (MO)	not used	not used	AY099919
Tamarix usneoides E. Mey. ex Bunge	Namibia, *M. Olson 717* (MO)	AY099935	AY099902	AY099922

Appendix 2. Pairwise distances between Tamaricaceae taxa.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. *Tamarix ramosissima*	—	0.005	0.001	0.010	0.008	0.026	0.026	0.026	0.026	0.035	0.041	0.040	0.042
2. *Tamarix aucherana*		—	0.005	0.010	0.010	0.026	0.028	0.027	0.027	0.037	0.044	0.044	0.045
3. *Tamarix parviflora*			—	0.010	0.008	0.024	0.026	0.026	0.026	0.036	0.042	0.041	0.042
4. *Tamarix usneoides*				—	0.005	0.023	0.025	0.024	0.024	0.033	0.039	0.039	0.041
5. *Tamarix aphylla*					—	0.025	0.026	0.027	0.027	0.036	0.043	0.041	0.043
6. *Myrtama elegans*						—	0.013	0.013	0.012	0.031	0.037	0.038	0.040
7. *Myricaria alopecuroides*							—	0.002	0.002	0.035	0.038	0.038	0.040
8. *Myricaria squamosa*								—	0.001	0.034	0.037	0.038	0.040
9. *Myricaria bracteata*									—	0.034	0.038	0.038	0.039
10. *Hololachna songarica*										—	0.021	0.022	0.022
11. *Reaumuria hirtella*											—	0.017	0.017
12. *Reaumuria turkestanica*												—	0.002
13. *Reaumuria cistoides*													—

REVISION OF THE MADAGASCAN ENDEMIC *STAPELIANTHUS* (APOCYNACEAE) BASED ON MOLECULAR AND MORPHOLOGICAL CHARACTERS[1]

P. V. Bruyns[2] *and C. Klak*[2]

Abstract

The genus *Stapelianthus* Choux (Asclepiadoideae–Ceropegieae), which is endemic to the arid southern parts of Madagascar, is revised and seven species are recognized. Morphological characters and characters derived from one chloroplast gene region (*trn*L-*trn*F) and one nuclear gene region (ITS1) are used in a combined analysis to show that, in its present circumscription, *Stapelianthus* is a monophyletic entity. The molecular characters clearly suggest that the species of *Stapelianthus* form a distinct evolutionary lineage from the remainder of the stapeliads in Africa. However, there are relatively few characters separating the species. Consequently, within the genus the relationships remain largely unresolved and are weakly supported where they are resolved. Although the genus remains morphologically difficult to circumscribe, it is defined by its unique coronal structure. *Stapelianthus calcarophilus* Morat is placed in synonymy under *S. arenarius* Bosser & Morat and *S. hardyi* Lavranos under *S. montagnacii* (Boiteau) Boiteau & Jean Bertrand. Lectotypes are selected for *S. insignis* Desc. and *S. decaryi* Choux.

Key words: Apocynaceae, Madagascar, phylogeny, *Stapelianthus*.

The stapeliads of Madagascar have been somewhat neglected. This is despite the fact that publications on Madagascan plants have been appearing since the middle of the 17th century, and therefore one must assume that botanical exploration of the island began even before this. Succulents have not been ignored, and it seems that the rich variety of aloes has been investigated and written about at least since early in the 19th century. The first species of stapeliad was discovered by Raymond Decary, provincial Commissioner of the southern district of Madagascar, in January 1918 near Beloha (P records). This was the very unusual plant described as *Trichocaulon decaryi* Choux in 1932. Within ten years of his first discovery of a stapeliad, Decary had found another two, one near Ambovombe and another near Fort Dauphin. The first of these was described as *Stapeliopsis madagascariensis* Choux in 1931 but, since the generic name had already been used by N. S. Pillans in 1928, *Stapeliopsis* Choux was illegitimate. Choux then moved this species to a new genus, *Stapelianthus* Choux (in White & Sloane, 1933), and in 1934 he described the third species found by Decary as *Stapelianthus decaryi* Choux.

After this, it was some years until Pierre Montagnac, Chief of the provincial agricultural service in Tulear, discovered *S. montagnacii* (Boiteau) Boiteau & Jean Bertrand in 1940 near Tulear and, in 1957, showed flowering specimens of the remarkable *S. insignis* Descoings to Bernard Descoings, who was then the resident botanist in Tananarive. It is in this area, i.e., the southwest and west, where further species have been found more recently.

Stapelianthus has never been accurately defined, and this may have led P. Boiteau to describe *S. montagnacii* first as a member of *Stapelia* L., an error which was fairly soon rectified. Subsequent confusion also arose when R. A. Dyer (1966) moved *Stapelia choanantha* Lavranos & H. Hall to *Stapelianthus*, and Leach (1968) followed along soon afterward with *Stapelianthus baylissii* L. C. Leach, a species which is closely allied to *S. choanantha*. Both of these are native to the Cape Province of South Africa. Rauh and Wertel (1968) showed quite clearly that these two species had little in common with the Madagascan species of *Stapelianthus*, but only in 1978 were they moved to *Tridentea* by Leach (Leach, 1978) and *Stapelianthus* was once more restricted to species endemic to Madagascar. Decary's earliest discovery, the peculiar *Trichocaulon decaryi*, was transferred to *Stapelianthus* in

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1961 so that this then became the only genus of stapeliad represented on the island.

When describing *Stapeliopsis madagascariensis*, Choux (1931) mentioned that the organization of the flower approaches that of *Caralluma* R. Br. (with the corona as in *C. dependens* N. E. Br.) and that the general impression is similar to that of *Stapelia*. His account (Choux, 1934) of *Stapelianthus decaryi* was extremely detailed, but there he did not discuss further the relationship with other African stapeliads or make clear what characteristics are shared by the two species he placed in *Stapelianthus*. White and Sloane (1937) suggested that *Stapelianthus* is most closely allied to *Huernia* and they stated how, in their opinion, the two genera differed. As evidence for the relationship with *Huernia*, they mentioned the "leafless" stems, their "appearance" and habit of growing in "large crowded tufts" [*S. decaryi*], the "small fascicles at the very base of the stems" in which the flowers arise and in the flowers the "tubular to campanulate shapes, with the inner corolla surface papillate" and the "sinuses between the corolla lobes projected into small intermediate points" (White & Sloane, 1937: 961). This view appears to have been reinforced subsequently by the discovery of species such as *S. insignis* and *S. keraudreniae* Bosser & Morat, which have considerably extended the range of corolla shapes found in *Stapelianthus* and revealed unexpected further parallels with *Huernia* R. Br. (compare flowers of *H. erectiloba* L. C. Leach and *S. insignis*; *H. zebrina* N. E. Br. and *S. keraudreniae*). The inclusion of *S. pilosus* Lavranos & D. S. Hardy in *Stapelianthus* seemed to substantiate this relationship yet further since, as White and Sloane (1937) already indicated, the remarkable stems of this species are very suggestive of those of *Huernia pillansii* N. E. Br. Thus Leach (1988: 3) considered that *Huernia* and *Stapelianthus* were most closely related among the stapeliads, though he also expressed the novel view (presented without evidence) that *Tavaresia* was related to both.

The genus *Stapelianthus* was reviewed by Morat (1994, 1995) and Rauh (1998). Both authors recognized nine species and one subspecies. However, neither of these authors assessed critically the relationships of *Stapelianthus* to the other genera of the stapeliads, and they both reiterated the view of White and Sloane (1937) that *Huernia* is the closest relative of *Stapelianthus*, without presenting any new evidence for this.

Meve and Liede (2002) included a single species of *Stapelianthus* (*S. decaryi*) in their molecular survey of the stapeliads. However, their results (e.g., their fig. 4) did not resolve its relationships to other genera.

Many of the features mentioned by White and Sloane (1937) and other authors are common to a broader range of genera than just *Huernia* and *Stapelianthus*, and this is also true of other characters that were not considered before. This leads one to suspect that *Huernia* is possibly not the closest living relative of *Stapelianthus*. However, our survey of morphological features did not throw enough light on the relationships of *Stapelianthus* or on the relationships within the genus. Consequently, we undertook a molecular investigation, using all the species in the genus, with characters of one chloroplast gene and one nuclear gene.

This study aims, therefore, by using both morphological and molecular characters, to address three issues: is *Stapelianthus* monophyletic, to which genera is *Stapelianthus* most closely related, and what are the relationships among the species of *Stapelianthus*.

Materials and Methods

Material was examined from the herbaria BM, BOL, K, MO, P, PRE, and TAN. For the SEM figures, material from living specimens was prepared as described in Bruyns (1993).

Ingroup and Outgroup Sampling

For the molecular analysis the seven species of *Stapelianthus* that are recognized here were included. Traditionally it has been assumed that *Huernia* is most closely related to *Stapelianthus* (White & Sloane, 1937). Exemplars were therefore chosen in the tribe Ceropegieae of the Asclepiadoideae from *Huernia* as well as from *Ballyanthus* Bruyns, *Duvalia* Haw., *Duvaliandra* M. G. Gilbert, *Orbea* Haw., *Tavaresia* Welw., and *Tridentea* Haw., since these were all shown in Bruyns (2000) to be possibly related to *Stapelianthus*. In addition, these are chosen as a broad sampling from the large, unresolved clade to which *Stapelianthus* belongs in Liede and Meve (2002, fig. 4). Although *Huernia* is the largest genus among the stapeliads (Leach, 1988), only a single species was used here since recent work (Nowell et al., unpublished) shows that *Huernia* is monophyletic. These recent investigations (Nowell et al., unpublished) included three species of *Tridentea* (in the strict sense of Bruyns, 1995), namely, *T. marientalensis* (Nel) L. C. Leach, *T. peculiaris* (C. A. Lückh.) L. C. Leach, and *T. virescens* (N. E. Br.) L. C. Leach, and found that this genus is also monophyletic. This did not corroborate the results of Meve and Liede (2002, fig.

4), where *T. virescens* is nested within *Orbea*, and it is strongly suspected that this is a consequence of misidentified material (since no voucher exists for their *T. virescens*). Therefore, here again a single species of *Tridentea* is included. These same studies, as well as that of Meve and Liede (2002), show that *Duvalia* is not monophyletic and that the monotypic *Ballyanthus* is nested within it. Consequently, two species of *Duvalia* (*D. maculata* N. E. Br. from southern Africa and *D. sulcata* N. E. Br. from Arabia) have been included here. In addition, representatives of more distantly related genera (*Baynesia* Bruyns, *Caralluma*, *Echidnopsis* Hook. f., and *Rhytidocaulon* P. R. O. Bally) were included. *Riocreuxia flanaganii* Schltr., a leafy, non-succulent member of the Ceropegieae that is sister to many of the more highly succulent members (according to Meve & Liede, 2002) was used to root the tree. Altogether, 21 species were included in the analysis (see Table 1).

DNA EXTRACTION AND AMPLIFICATION OF TEMPLATE DNA

Total DNA was isolated from fresh stem material of the 21 species by the method of Saghai-Maroof et al. (1984) as modified by Doyle and Doyle (1987).

The two DNA regions were amplified from total DNA by the polymerase chain reaction (PCR). The *trn*L-*trn*F and ITS1 regions were amplified using primers c and f (Taberlet et al., 1991) and primers ITS2 (Baldwin, 1992) and K18RC (5′-GCACGCGCGCTACACTGA-3′, Hedderson, unpublished), respectively. Twenty-five-μl reactions were prepared, which contained 19.625 μl of sterile water, 2.5 μl of 10× PCR buffer, 1 μl of 10 mM dNTPs in equimolar ratio, 0.75 μl of 10 μM primer, 0.5 μl of 25 mM $MgCl_2$, 0.125 μl of Taq DNA polymerase (5 U/μl), and 0.5 μl of genomic DNA. In general, a 10× dilution of the extraction product was used as template DNA. The thermal reactions were carried out as follows: first 2 min. at 97°C to ensure denaturation of double-stranded template DNA, 1 cycle; denaturing step of 97°C for 1 min., annealing step of 52°C for 60 sec., and extension step of 72°C for 2 min.; the preceding three steps were repeated 30 times and were finally followed by one extension step for 7 min. at 72°C to complete unfinished DNA strands. The reactions were cleaned using the QIAquick PCR purification kit from Qiagen, and the purified products were eluted in 30 μl of TE.

SEQUENCING AND ALIGNMENTS

Both strands of the PCR products were cycle sequenced, as per manufacturer's instructions, using the ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit from PE Biosystems. The primers used for the amplification were also used for the sequencing reactions. In addition, for some samples the internal *trn*L-*trn*F region primers d and e were used (Taberlet et al., 1991). The samples were run on an Applied Biosystems 377 automated DNA sequencer.

Data files were assembled and edited using Chromas Version 1.43 (McCarthy, 1996–1997) and GeneDoc (Nicholas & Nicholas, 1997). Sequences were aligned by eye. Ambiguous positions were coded using appropriate IUPAC ambiguity symbols so as to maximize the retention of information. Gaps were coded as suggested by Simmons and Ochoterena (2000). Their method of simple indel coding is followed in this study. The alignments of the sequences are available from the authors in Nexus format.

CLADISTIC ANALYSES

The data matrix was analyzed using PAUP* version 4.0b4a (PPE) (Swofford, 2000) under the maximum parsimony optimality criterion with all parsimony-uninformative characters excluded and all characters unordered. Initially, each DNA region was analyzed separately. The first step in each of these analyses involves an initial sweep of the tree space in an attempt to increase the chances of identifying all islands of most parsimonious trees. For this, one thousand consecutive heuristic searches were conducted using random stepwise taxon addition with tree-bisection-reconnection (TBR) branch swapping, MULTREES and steepest descent in effect. Branches of zero length were collapsed. During each replicate only two trees were saved. All of these trees were then used as starting trees for the next search with TBR branch swapping, MULTREES and steepest descent in effect. Again, branches with maximum length of zero were collapsed. To assess clade support, the data set was analyzed using the jackknife option as implemented in PAUP*. Farris et al. (1996) have shown that with a removal probability of 36.79% (~ 37%, Backlund & Bremer, 1997) jackknife values of more than 63% correspond to a node supported by at least one uncontradicted character. Therefore, the percentage of deleted characters for all jackknife analyses in this study was fixed at 36.79%. Only groups with frequency greater than 50% were retained. Nodes with jackknife values greater than

Table 1. Taxa employed in molecular analysis with Genbank accession numbers.

Species	Origin	Collector and number	Genbank accession number for *trn*L-*trn*F sequence	Genbank accession number for ITS sequence
Riocreuxia flanaganii Schltr.	South Africa, near Butterworth	*Bruyns 8995* (E)	AJ519957	AJ519978
Ballyanthus prognathus (P.R.O. Bally) Bruyns	Somalia	*Reynolds* (BOL)	AJ519956	AJ519977
Baynesia lophophora Bruyns	Namibia, Baynes Mountains	*Bruyns 8000* (BOL, K, MO, PRE)	AJ519951	AJ519972
Caralluma crenulata Wallich	Myanmar, near Mandalay	*Bruyns 8808*	AJ519954	AJ519975
Duvalia maculata N. E. Br.	South Africa, near Victoria West	*Bruyns 5109* (BOL)	AJ519958	AJ519979
Duvalia sulcata N. E. Br.	Yemen	*Řičánek & Hanáček 286*	AJ519962	AJ519983
Duvaliandra dioscoridis (Lavranos) M. G. Gilbert	Socotra	*Miller 10461* (E)	AJ519953	AJ519974
Echidnopsis malum (Lavranos) Bruyns	Ethiopia, near Dire Dawa	*Bruyns 8490* (E)	AJ519950	AJ519971
Huernia verekeri subsp. *pauciflora* L. C. Leach	Mozambique, near Beira	*Bruyns 7681* (MO)	AJ519960	AJ519981
Orbea araysiana (Lavranos & Bilaidi) Bruyns	Yemen, Jebel Arays	*Řičánek & Hanáček 284* (K)	AJ519952	AJ519973
Orbea ubomboensis (I. Verd.) Bruyns	South Africa, near Messina	*Bruyns 7471* (K, MO)	AJ519961	AJ519982
Rhytidocaulon ciliatum Hanáček & Řičánek	Yemen	*Řičánek & Hanáček 264*	AJ519955	AJ519976
Stapelianthus arenarius Bosser & Morat	Madagascar	*Bruyns 5954* (K)	AJ519949	AJ519969
Stapelianthus decaryi Choux	Madagascar	*Bruyns 6191* (BOL)	AJ519944	AJ519965
Stapelianthus insignis Descoings	Madagascar	*Bruyns 6208* (E)	AJ519945	AJ519966
Stapelianthus keraudreniae Bosser & Morat	Madagascar	*Alp s.n.* (BOL)	AJ519947	AJ519968
Stapelianthus madagascariensis (Choux) Choux	Madagascar	*Bruyns 5958* (MO)	AJ519942	AJ519963
Stapelianthus montagnacii (Boiteau) Boiteau & Jean Bertrand	Madagascar	*Bruyns 6195* (BOL)	AJ519943	AJ519964
Stapelianthus pilosus Lavranos & D. S. Hardy	Madagascar	*Bruyns 5959* (BOL)	AJ519946	AJ519967
Tavaresia barklyi (Th.-Dyer) N. E. Br.	Botswana, near Serowe	*Bruyns 6432* (BOL)	AJ519948	AJ519970
Tridentea peculiaris (C. A. Lueckh.) L. C. Leach	South Africa, near Vredendal	*Bruyns 1293*	AJ519959	AJ519980

or equal to 63% are regarded as supported by the data (Farris et al., 1996; Backlund & Bremer, 1997; Bakker et al., 1998).

The separate analyses showed that there were no areas of conflict between the data sets. Where differences existed, these were statistically poorly supported. Therefore, in addition to the separate analyses, the following combined analyses were performed. These used the same PAUP settings as the individual analyses.

COMBINED ANALYSIS 1. A data set consisting of the *trn*L-*trn*F and ITS1 was constructed for the 21 taxa.

COMBINED ANALYSIS 2. A data set consisting of the *trn*L-*trn*F, ITS1, and 19 morphological characters (as given in Table 3) was constructed for the 21 taxa.

MORPHOLOGICAL CHARACTERS AND THEIR CODING (NUMBERED AS IN TABLE 3)

Stems

Macroscopic observations

1. Stems erect to shortly decumbent = 0; prostrate = 1.

Stems in *Stapelianthus* are procumbent in most species, often with ascending apices, though plants tend to become more decumbent if more exposed to sunlight (those deeply hidden in bushes maintaining the most horizontal habit). Only in *S. decaryi* are they decumbent-erect with a shortly prostrate base.

The stems tend to form dense clumps, in *S. montagnacii* and *S. decaryi* up to 1 m or more in diameter, in others rather smaller (up to 0.3 m), and only in *S. pilosus* do they usually form rather diffuse clusters. Rhizomatous stems (i.e., horizontal, underground stems) do not occur.

2. Stems 4- or 5-angled = 0; 6- or more-angled = 1.

The tubercles are arranged along the stems in 4 or sometimes 5 angles in *Stapelianthus arenarius* Bosser & Morat, *S. montagnacii*, *S. insignis*, and *S. keraudreniae*. In *S. arenarius* the angles are not very clear, but in the others the tubercles are joined into wings along the stems, which are thus noticeably square. In *S. madagascariensis* the tubercles are arranged into 4 to 6 angles, which in southern localities (e.g., Ambovombe to Tsihombe) often have a slender, rather cylindrical appearance, and in *S. decaryi* into 6 up to 8 angles. In both of these the primary tubercles are paired and for the first few nodes the stem is 4-angled, while only later are the tubercles arranged in alternating whorls of 3 (or 4).

In *S. pilosus* the rather small, conical tubercles are densely packed on the stems with no discernable arrangement into angles. Seedlings of this species have not been studied to find out how this arrangement begins. In this species the stems are uniformly green (uniformly purplish if exposed to sunlight) and smooth.

In the others the stems are mottled with purple-brown on a cream to silver-gray or greenish background. In all of these except *S. decaryi* the surface is bullate (most markedly so in *S. arenarius*), especially toward the edges of the tubercles. In all of them, including *S. decaryi*, the tubercles are broad and somewhat flattened, narrowing abruptly into the leaf. In most cases the tubercle has a groove on the upper surface toward the base.

Although variable in thickness (from 3 to 15 mm), the stems are generally slender in comparison with most African stapeliads (except for those of *S. pilosus*, which more closely correspond to other African species in thickness).

Microscopic observations of the epidermis of the stem (Fig. 1)

3. Surface of stem not bullate = 0; bullate = 1.

The bullate surface of the stems of many *Stapelianthus* is most unusual. On the African continent this phenomenon is rare among stapeliads, where it is known only in *Echidnopsis leachii* Lavranos, the recently described *Baynesia lophophora* Bruyns, and the few species of *Rhytidocaulon* P. R. O. Bally. Bullate stem surfaces are, however, found in many asclepiads from Madagascar: many of the succulent and practically leafless species of *Cynanchum* from Madagascar exhibit it, as do also several highly succulent species of *Ceropegia*, both from the arid southwest and elsewhere on the island.

In *Stapelianthus pilosus* the epidermal cells on the tubercle are irregularly shaped with flat outer walls. On the leaf, the cells are long and narrow, each with a conspicuous, rounded papilla toward or at the upper end (toward the tip of the leaf).

In the other species examined (*S. insignis*, *S. keraudreniae*, *S. madagascariensis*), the epidermal cells are ± isodiametric, often raised into a low, rounded, central papilla with a few cells raised into conical papillae along the edge of the leaf toward its base. Other cells on the leaf are ± as on the tubercle.

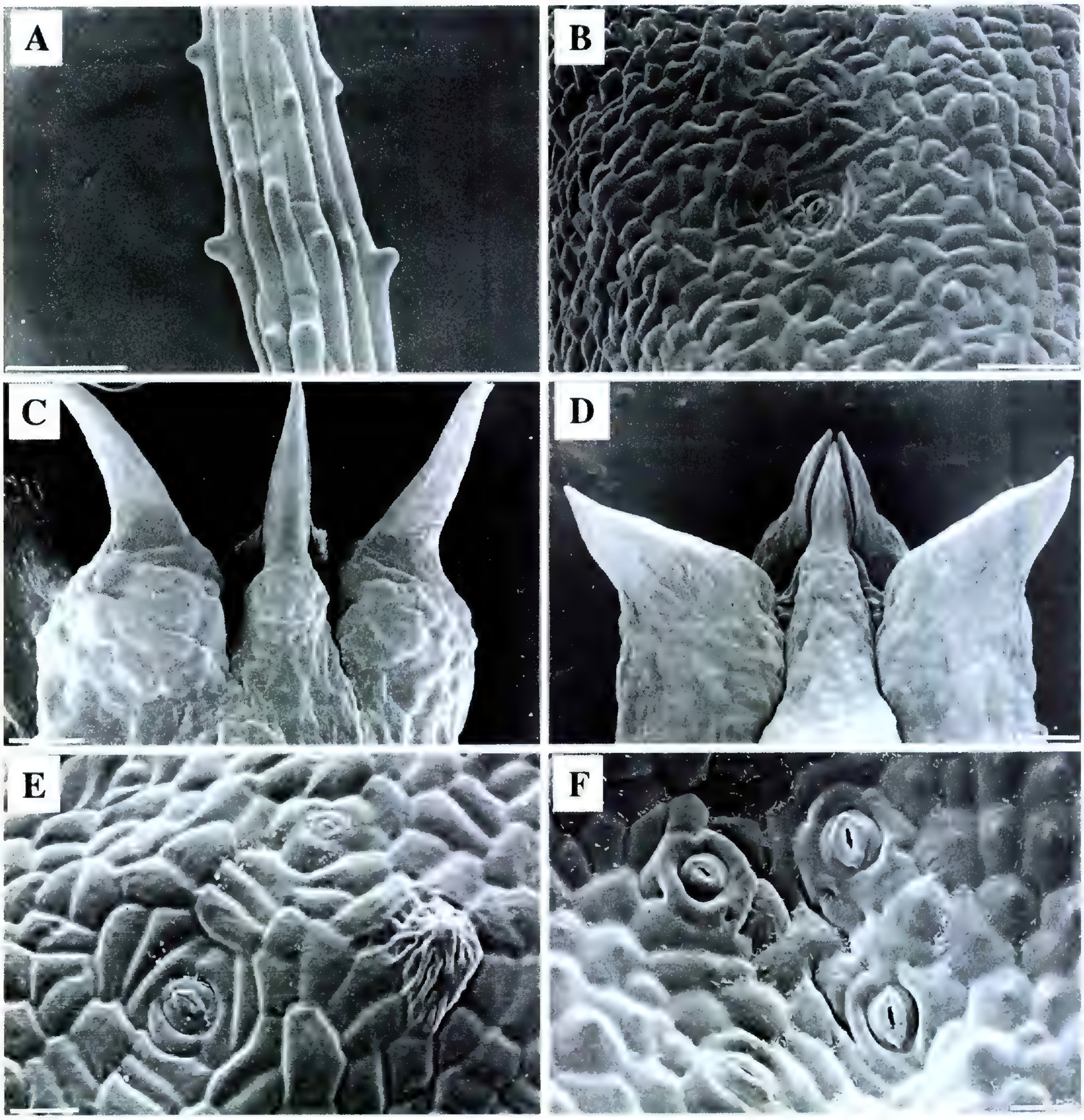

Figure 1. SEM views of surfaces of stems and leaves of *Stapelianthus*. *S. pilosus* (*PVB 5959*):—A. Surface of "leaf."—B. Surface of tubercle with stoma. —C. *S. arenarius* (*PVB 5954*), leaves and wrinkled surface of tubercle. —D. *S. insignis* (*PVB 5957*), leaves and wrinkled surface of tubercle. —E. *S. madagascariensis* (*PVB 5958*), stomata and cells with flat outer walls. —F. *S. keraudreniae* (material ex hort.), stomata and cells with outer walls with small central papillae. Scale bars: A, 50 μm; B, 100 μm; C, 0.6 mm; D, 1 mm; E, F, 25 μm.

Leaf rudiments

4. Leaf or leaf rudiment clearly differentiated from the apex of the tubercle (if present) = 0; not clearly differentiated from the apex of the tubercle = 1.

Leaf rudiments are present in all species, but are always very small and are not clearly differentiated from the apex of the tubercle. They dry out rapidly but persist as a whitish husk (for a long time in *Stapelianthus pilosus*, in the others more fleetingly) until eventually falling off. Initially erect, the leaf rudiment gradually spreads with the growth of the tubercle. In all species except *S. pilosus*, the stronger growth of the upper surface of the tubercle pushes the leaf rudiment into a descending position.

In *Stapelianthus pilosus* the tubercle tapers gradually into a slender, filiform, ± cylindrical leaf rudiment 2.5–4.0 mm long whose base is clearly marked by the beginning of the small papillae mentioned above. In *S. decaryi* the leaf rudiment is nar-

rowly conical, slightly flattened above, and 2–4 mm long. In all the others it is a small, ovate-lanceolate to narrowly deltoid (narrowly lanceolate in *S. arenarius*) structure 1–2 mm long, which is flat on the upper surface and keeled below and merges with the apex of the tubercle (perched on the broad apex of the tubercle in *S. arenarius*). There is no trace of blade or midrib in any of them.

5. Stipular denticles or stipular gland present = 0; absent = 1.

Stipules are absent throughout *Stapelianthus*.

Inflorescences

6. Inflorescences borne toward the apex of the stem = 0; toward the base = 1.
7. Inflorescences numerous per stem = 0; one per stem = 1.

In *Stapelianthus* inflorescences arise near the base of the younger stems and so are usually found toward the outer edge of the clump or ± on top of the mat. Several flowers are borne in very slow succession, usually with only one flower in a given inflorescence opening at a time. There is rarely more than one inflorescence per stem. The organization of flowers in the inflorescence is typical of simple stapeliad inflorescences, as for *Echidnopsis* (Bruyns, 1988). The inflorescences may be somewhat sunken into the stems in *S. arenarius*, but they are otherwise superficial. The bracts are lanceolate to deltate and rarely possess very small lateral outgrowths toward the base.

Flowers

Corolla

8. Corolla ± rotate with small tube = 0; campanulate to tubular = 1.
9. Corolla without distinct thickening around mouth of tube = 0; with at least somewhat thickened annulus around mouth of tube = 1.

There is a remarkable degree of variation in the geometry of the corolla within this small genus of seven species. From nearly flat in *Stapelianthus arenarius*, shallowly campanulate (*S. madagascariensis*) to more deeply campanulate (*S. montagnacii*), it is modified to rotate with a conspicuous annulus in *S. keraudreniae*, bicampanulate in *S. insignis*, and deeply tubular in *S. decaryi*.

The flowers vary between 10 and 35 mm in diameter and so are neither large nor very small. Most of them are variously spotted both inside and outside with dark purple-red/brown on a creamy or yellow background. In *Stapelianthus montagnacii* most of the flower is uniformly colored inside and only in the base of the tube is it mottled, while the exterior is often mottled as well. The outer surface is smooth, but the inner surface is papillate in all species. In *S. decaryi* the inner surface is densely covered with stout, columnar papillae each with a black summit, whose apical cell is modified into an acute seta. In *S. montagnacii*, *S. madagascariensis*, and, to a lesser extent *S. pilosus*, the papillae are long and slender. They form quite a dense beard on the lobes at least in *S. montagnacii* and are more scattered in the other two. The apical seta on each papilla is obtuse in *S. madagascariensis* and spherical in *S. montagnacii*. In *S. keraudreniae* small, scattered papillae are found all over the corolla with longer ones only toward the edges of the lobes; in *S. insignis* small, conical papillae are located around the edges of the lobes only.

Several species exhibit a thickening of the corolla around the mouth of the tube. Only in *S. insignis* and most noticeably in *S. keraudreniae* does this lead to a definite annulus, which is the most conspicuous feature of the flower in the latter.

Gynostegium

10. Outer and inner corona partly fused on staminal tube = 0; separated on staminal tube and not at all fused = 1.
11. Outer corona lobes not exceeding height of gynostegium = 0; much exceeding height of gynostegium = 1.
12. Outer corona lobes not laterally fused to one another = 0; laterally at least somewhat fused to one another = 1.

Stapelianthus pilosus is the only species of *Stapelianthus* in which the outer corona lobes are somewhat laterally fused.

13. Corpuscles secreted at level below highest point on style head = 0; corners of style head secreting corpuscles somewhat above rest of style head = 1.

In all species of *Stapelianthus* the gynostegium is perched upon a stipe, which is short in most but up to 1 mm or more long in *S. decaryi*.

The outer corona lobes have a characteristic shape that is unique to *Stapelianthus*: they are always broad and dorsiventrally flattened, erect above the base and remaining close laterally so as to outline a deep cup in the base of which the inner lobes are situated. In *S. pilosus* they are fused for nearly

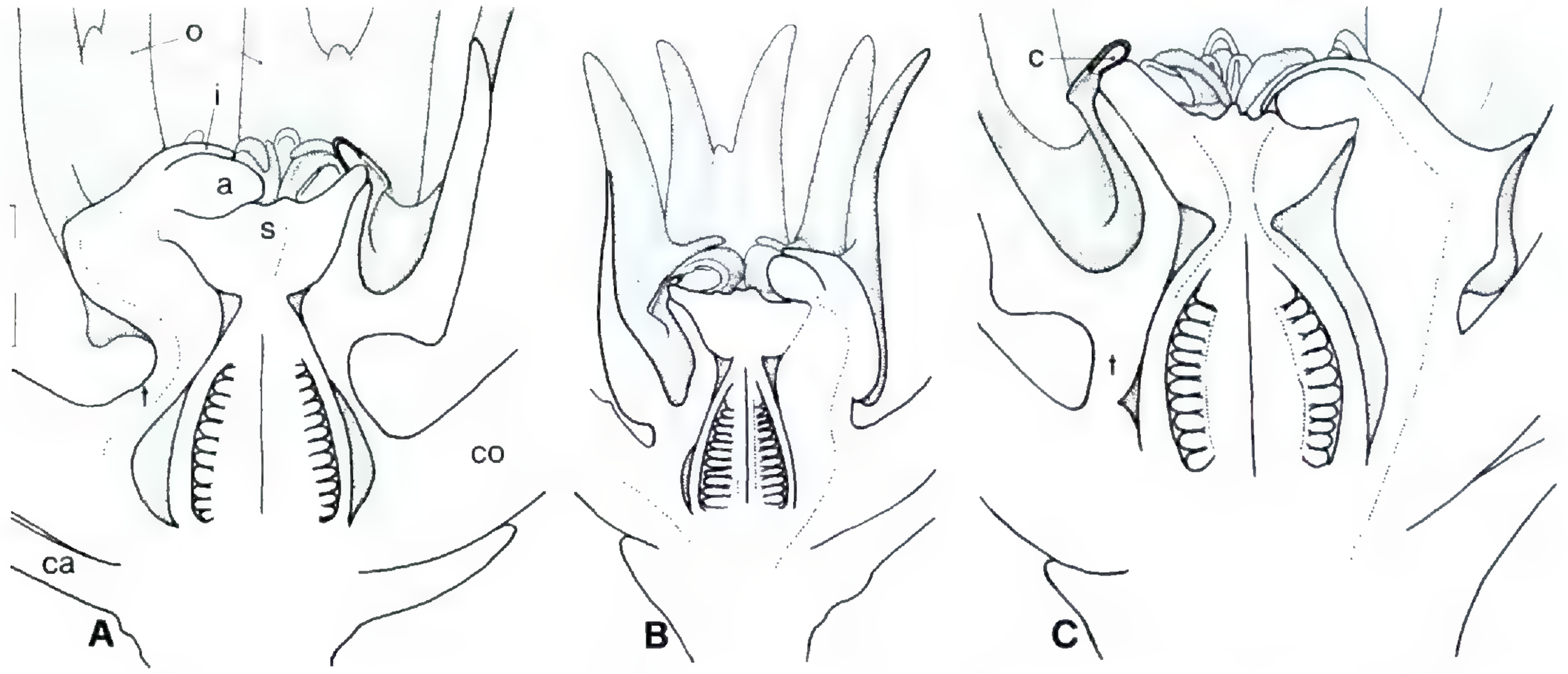

Figure 2. Half-flowers in *Stapelianthus*.—A. *S. decaryi* (*PVB 5960*). —B. *S. pilosus* (*PVB 5959*). —C. *S. insignis* (*PVB 5957*). Scale bar: A–C, 1 mm (at A). a = anther; c = corpuscle; ca = calyx; co = corolla; i = inner corona lobe; o = outer corona lobe; s = style head; t = staminal tube.

half their length, while in all the others they are free nearly to the base.

The inner corona lobes are short, incumbent on the anthers, and do not usually exceed them. They are joined by a ridge of tissue near their bases to the outer series but have no dorsal horns or projections.

The anthers are quadrate and horizontal to descending but have sometimes been observed in *S. pilosus* to possess a short, acute, apical appendage.

The style head in *Stapelianthus* is somewhat concave above, as can be seen in Figure 2. Situated between the anthers are five high points that are mostly well above the level of the center, though somewhat less so in *S. pilosus* than in the other species. It is on these high points that the corpuscles are secreted. Between these high points are five lower areas into which the anthers are pressed. These lower areas are usually just below the level of the center of the style head. The anthers are then horizontal on top of the style head, with the inner corona lobes descending toward the center, most noticeably so in *S. montagnacii* and *S. insignis*. The outer edge of the five highest areas (between the anthers and bearing the corpuscles) slopes upward so that the corpuscle is thus also held facing obliquely inward, and this is true even in *S. pilosus*. The pollinia lie on the region sloping away from this highest area and also usually descend slightly toward the center.

The ontogeny of the staminal coronas has been observed in *Stapelianthus insignis*. A small transverse ridge first appears beneath each guide rail. These ridges develop into the outer corona lobes. At a slightly later stage a further small ridge develops in the middle of the back of each anther just slightly above the level of the early stages of the outer lobes. These give rise to the inner corona lobes. Both series of lobes continue to grow, with the outer lobes spreading laterally as well so that eventually adjacent outer lobes nearly touch behind the inner lobes. The relative positions of the mature corona lobes of the two series can be seen in Figure 2.

Pollinaria

14. Pollinia ellipsoidal = 0; D-shaped = 1.
15. Pollinia broader than long = 0; longer than broad = 1.
16. Pollinia with insertion crest exactly along edge = 0; with insertion crest twisted onto dorsal surface = 1.
17. Caudicle not widening toward apex = 0; broader toward apex and somewhat spathulate beneath pollinium = 1.

In all species of *Stapelianthus* the pollinia are longer than broad. In *S. pilosus* the pollinia are ellipsoidal and relatively small, with broad corpuscles bearing small wings. In all other species of *Stapelianthus* the pollinia are larger and D-shaped, with the corpuscle widening toward the apex and flanked by long, narrow wings. The caudicle is usually much broadened toward the top, with the pollinium attached to the broadest, rather spathulate part. In all species the insertion crest is attached on the edge at the top of the pollinium, after which it twists around slightly onto the upper surface toward the middle of the pollinium.

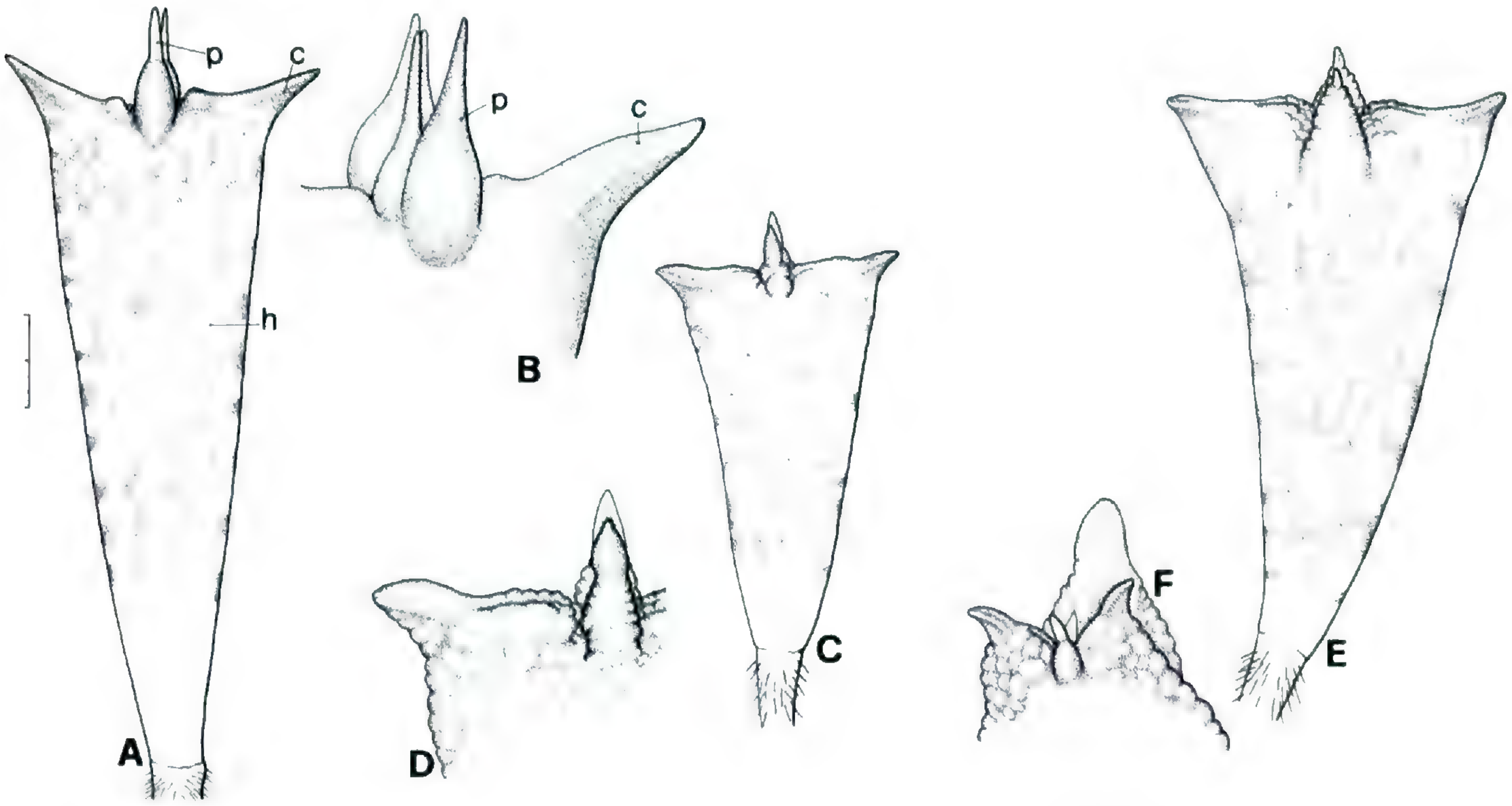

Figure 3. Seedlings in *Stapelianthus*.—A, C, E. Whole plantlet after ± 3 weeks. —B, D, F. Close-up of apex of plantlet. A, B, *S. decaryi* (*PVB 5960*). C, D, *S. madagascariensis* (*PVB 5958*). E, F, *S. arenarius* (*PVB 5954*). Scale bars: A, C, E, 2 mm (at A); B, D, F, 1 mm (at A). c = cotyledon; h = hypocotyl; p = primary leaf rudiment and tubercle.

Seedlings

18. Hypocotyl uniformly colored = 0; mottled = 1.
19. Cotyledon with ± spathulate to elliptic bladelet = 0; ± without any blade = 1.

Seed has been grown of *Stapelianthus arenarius*, *S. decaryi*, *S. insignis*, *S. montagnacii*, and *S. madagascariensis*. In all of them the hypocotyl is cuneiform (Fig. 3) and mottled with purple on a pale, creamy green background. The cotyledons are flattened above, ± deltoid, obtuse to acute, and, although much reduced, are still distinguishable from the hypocotyl. In *S. decaryi* the whole surface is smooth, the primary and secondary leaves are paired, and for the first 2 to 4 nodes the stem is 4-angled. In the others the surface is bullate, the upper surface of the cotyledonary tubercle is grooved toward the base, and for the first few nodes the stem is 4-angled. In *S. arenarius* the primary stem gradually bends toward the surface of the soil to assume a ± prostrate habit. This happens before the side branches develop.

Results

Sequence length in the chloroplast *trn*L-*trn*F region varied between 835 and 889 bp with the majority of species measuring 855 bp. Numerous indels were present in the *trn*L-*trn*F gene region. In this study all gaps were treated as single sites regardless of their length and were coded as binary characters to be added to the data matrix and included in the analyses. The longest insertion (17 bp) was recorded for *Duvalia maculata*, whereas the longest deletion (10 bp) was found in *Duvalia sulcata*. One indel was found to be parsimony informative.

The nuclear ITS1 region varied between 575 and 578 bp in length. Several species had single indels, and *Orbea ubomboensis* had an insertion of 3 bp. There were no informative indels.

Statistics, including numbers of variable positions and measures of consistency, are given for each analysis in Table 2. There were no areas of ambiguity in the alignment (available from the authors).

*trn*L-*trn*F ANALYSIS

The strict consensus (not shown) of the 19 trees recovered (L = 20, CI = 0.700, RI = 0.885, RC = 0.619) shows a monophyletic *Stapelianthus* (jackknife (JK) = 62) but without resolution among the species. Sister to *Stapelianthus* are the representatives of *Ballyanthus*, *Duvalia*, *Huernia*, *Orbea*, *Tavaresia*, and *Tridentea*. These, together with *Stapelianthus*, form a strongly supported but unresolved monophyletic group (JK = 81). *Baynesia* is the sister to this entire clade (JK = 90). Only 13 informative characters were found, including one indel.

Table 2. Summary of statistics for parsimony analyses of *Stapelianthus* and related taxa. CI = Consistency Index, RI = Retention Index, RC = Rescaled Consistency Index.

Analysis	Total characters	Indels	Variable characters	Informative characters	Tree length	No. of trees	CI	RI	RC
*trn*L-*trn*F	889	1	38	13	20	19	0.700	0.885	0.619
ITS1	578	—	69	35	62	28	0.677	0.823	0.558
Morphology	19	—	19	19	43	1358	0.442	0.788	0.348
Combined 1: *trn*L-*trn*F & ITS1	1467	1	107	48	85	5	0.659	0.824	0.543
Combined 2: *trn*L-*trn*F & ITS1 & morphology	1486	1	107	67	144	84	0.521	0.752	0.392

ITS1 ANALYSIS

The strict consensus (not shown) of the 28 trees recovered (L = 62, CI = 0.677, RI = 0.823, RC = 0.558) shows a highly supported monophyletic *Stapelianthus* (JK = 98) but with low resolution among the species. All the remaining stapeliads sampled are arranged in a polytomy of which *Stapelianthus* is the largest and best-supported clade. Here 35 informative characters were found.

Morphological analysis. The strict consensus (not shown) of the 1358 trees recovered (L = 43, CI = 0.442, RI = 0.788, RC = 0.348) shows a weakly supported and internally unresolved clade made up of all species of *Stapelianthus* and *Tavaresia* (JK = 66). Sister to *Stapelianthus* are the representatives of *Ballyanthus*, *Duvalia*, *Duvaliandra*, *Huernia*, *Orbea*, and *Tridentea* (i.e., similar to the results of the *trn*L-*trn*F analysis) in a clade of support with JK = 74. Only 19 informative characters were found.

Combined analysis 1 (trn*L*-trn*F and ITS genic regions).* The strict consensus (Fig. 4) of the five trees recovered (L = 85, CI = 0.659, RI = 0.824, RC = 0.543) shows a well-resolved, and in many parts also well-supported, phylogeny. *Stapelianthus* is monophyletic (JK = 100) in which *S. insignis*, *S. madagascariensis*, and *S. montagnacii* form a poorly supported clade (JK = 62). Sister to *Stapelianthus* is an unsupported clade made up of the

Table 3. Character states for the 19 morphological characters used in cladistic analysis.

Species	Characters			
	1–5	6–10	11–15	16–19
Riocreuxia flanaganii	0?000	00100	00000	0000
Ballyanthus prognathus	00010	00011	01001	01??
Baynesia lophophora	00100	00100	00000	0000
Caralluma crenulata	00000	010?0	0000?	0000
Duvalia maculata	00010	11011	01001	0101
Duvalia sulcata	00011	11011	01001	0101
Duvaliandra dioscoridis	00011	?1010	0?001	01??
Echidnopsis malum	11000	00100	1100?	0000
Huernia verekeri subsp. *pauciflora*	11011	11001	01001	0101
Orbea araysiana	00011	00010	00011	1101
Orbea ubomboensis	00010	00010	00011	1101
Rhytidocaulon ciliatum	00100	00000	00000	0000
Stapelianthus arenarius	10111	11000	10111	1111
Stapelianthus decaryi	01011	11100	10111	1111
Stapelianthus insignis	10111	11110	10111	1111
Stapelianthus keraudreniae	10111	11010	10111	1111
Stapelianthus madagascariensis	10111	11100	10111	1111
Stapelianthus montagnacii	10111	11100	10111	1111
Stapelianthus pilosus	01011	11?00	11101	1???
Tavaresia barklyi	01011	11100	10111	1101
Tridentea peculiaris	00001	11010	00011	1100

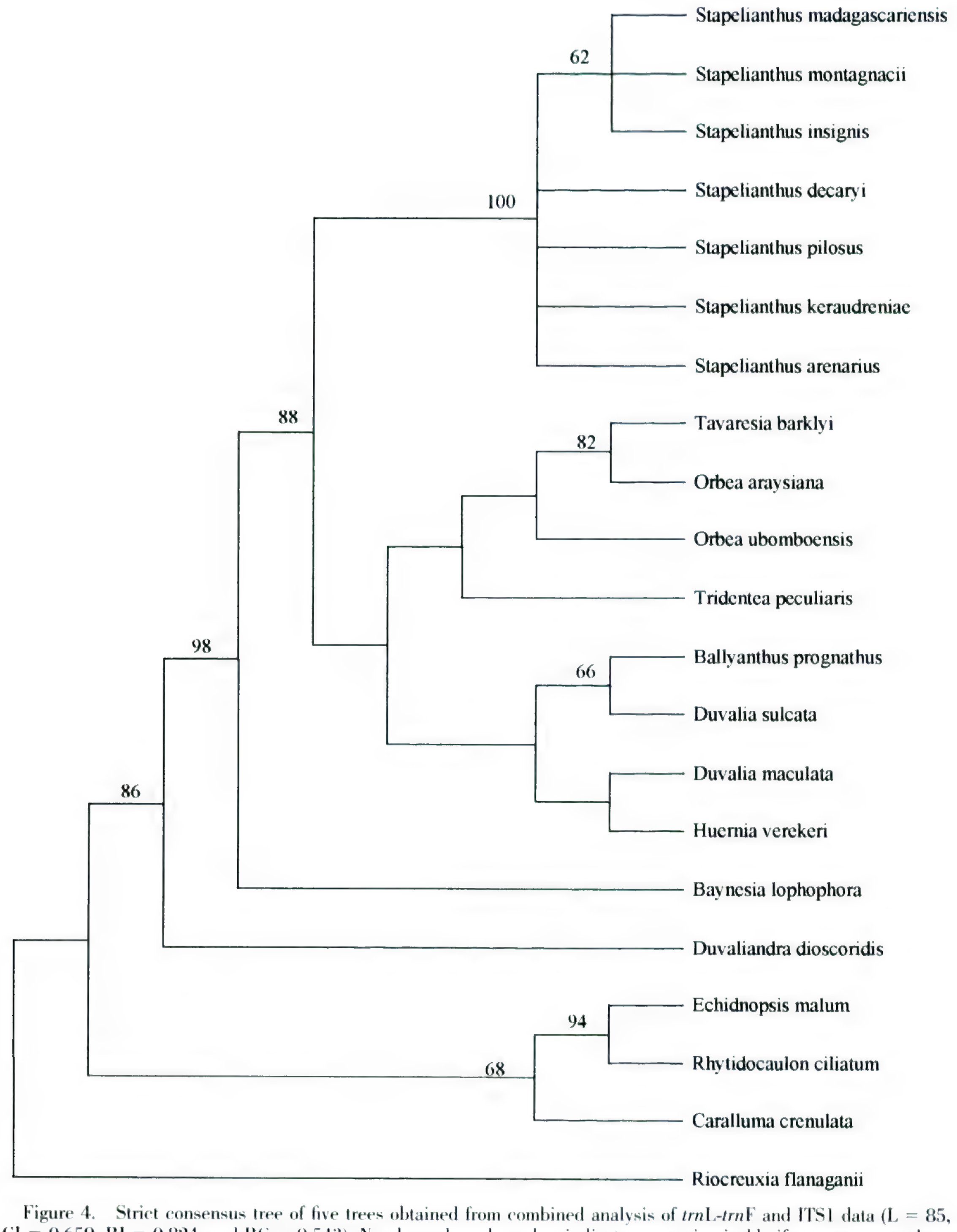

Figure 4. Strict consensus tree of five trees obtained from combined analysis of *trn*L-*trn*F and ITS1 data (L = 85, CI = 0.659, RI = 0.824, and RC = 0.543). Numbers above branches indicate supporting jackknife percentages, where they are above 50%.

representatives of *Ballyanthus*, *Duvalia*, *Huernia*, *Orbea*, *Tavaresia*, and *Tridentea*, so that no close relatives of *Stapelianthus* appear to be among these taxa. The phylogram based on one of the five trees (Fig. 5) shows an especially long branch at the base of *Stapelianthus*, which again suggests that it is very distinct from the other African taxa.

Combined analysis 2 (trn*L*-trn*F*, *ITS genic regions, and morphology).* The strict consensus (Fig. 6) of the 84 trees recovered (L = 144, CI =

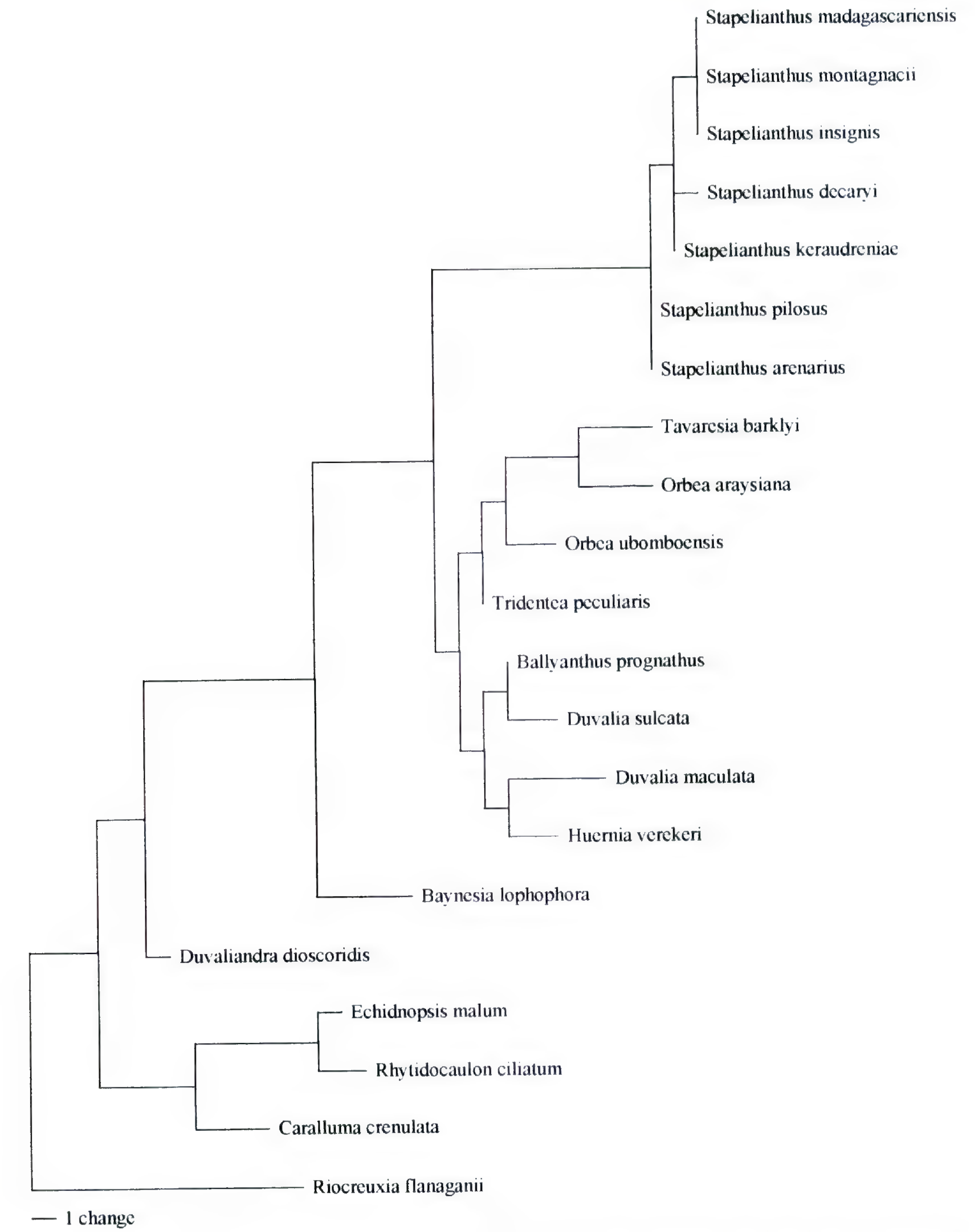

Figure 5. Phylogram based on one of five trees obtained from combined analysis of *trn*L-*trn*F and ITS1 data. The lengths of the branches are drawn in proportion to the number of character changes.

0.521, RI = 0.752, RC = 0.392) shows again a well-supported *Stapelianthus* (JK = 100). Within it there is a clade consisting of *S. arenarius*, *S. insignis*, *S. keraudreniae*, *S. madagascariensis*, and *S. montagnacii* (JK = 74) to which the remaining two species are sisters. *Tavaresia* resolves here as a sister to *Stapelianthus* but with very weak support (JK = 56), whereas based on molecular characters alone (combined analysis 1) it was sister to *Orbea araysiana* (JK = 82).

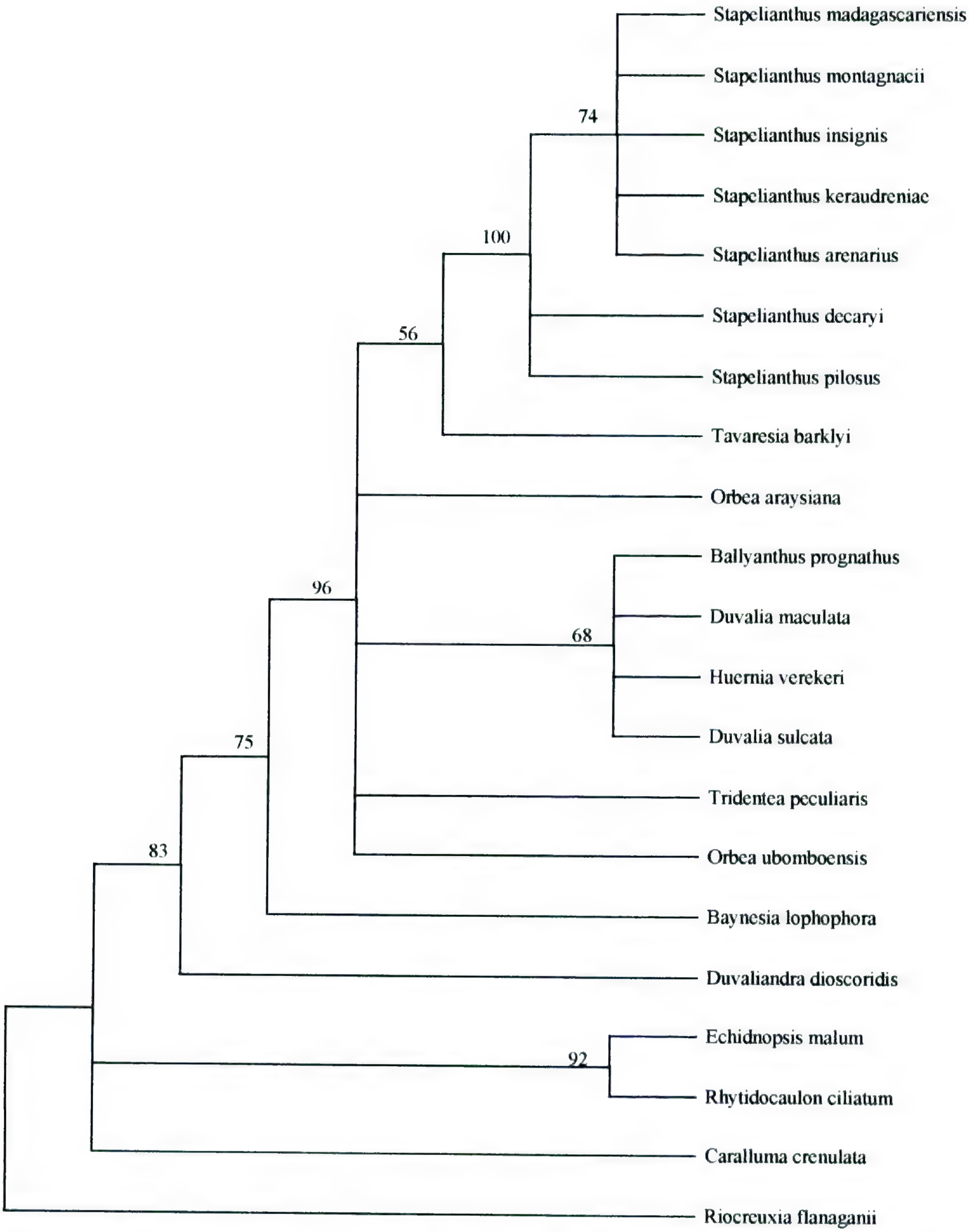

Figure 6. Strict consensus tree of 84 trees obtained from combined analysis of *trn*L-*trn*F, ITS1, and morphological data (L = 144, CI = 0.521, RI = 0.752, and RC = 0.392). Numbers above branches indicate jackknife percentages.

Discussion

Our morphological survey outlines the wide variation that is found in most features of members of *Stapelianthus*. It has shown that the defining characteristics of *Stapelianthus* are the spineless stems combined with the ascending to erect, deeply bifid outer corona lobes, which form a cup around the top of the gynostegium containing entirely the small and horizontal to slightly descending inner lobes.

1. PHYLOGENETIC RELATIONSHIPS

Morphological evidence. In the morphological analysis (not shown) *Tavaresia* becomes part of the *Stapelianthus* clade (although weakly supported, JK = 66). One might hesitate at this conclusion, especially because of the unusual leaf rudiments of *Tavaresia*. While the leaf rudiments of many *Stapelianthus* bear some resemblance to those of *Huernia*, those of *Tavaresia* appear to be very different. However, the epidermal cells on the filiform leaf rudiments of *S. pilosus* are similar to those observed on young leaf rudiments of *Tavaresia* (and also documented for *Hoodia* in Bruyns, 1993, fig. 4D, F). They seem to represent a transitional stage from normal epidermal cells to the elongated ones found on all stapeliad spines (including those of *Tavaresia*). They are, in fact, rather dissimilar to those on the filiform leaf rudiments of *Huernia pillansii*, which is the species of *Huernia* bearing the greatest vegetative similarity to *S. pilosus*. The pair of spines at the base of each main spine in *Tavaresia* are not stipules (Meve & Albers, 1990) and should possibly be interpreted as an extreme form of the hastate leaves found in some forms of *Ceropegia linearis* E. Mey. or in *Microloma sagittatum* (L.) R. Br., a random phenomenon in various unrelated groups, which is probably of little taxonomic significance at higher levels. It may be added that the flower of *Stapelianthus decaryi* also has a similar shape and papillate surface inside to the flower in *Tavaresia*.

In assessing the validity of this result, five further characters deserve mention. (Here the genera *Duvalia*, *Huernia*, *Orbea*, *Stapelianthus*, and *Tavaresia* are all brought into consideration.)

(1) Outer corona

In *Huernia* the outer corona descends from its point of attachment to the staminal column toward the base of the corolla, while in *Duvalia* it remains more or less horizontal: at any rate in both it keeps entirely away from the remainder of the gynostegium. This is different from the position in *Orbea*, *Stapelianthus*, and *Tavaresia*.

The cup formed by the outer corona in *Tavaresia* is fused toward the base into a single structure and the same is true in *Stapelianthus pilosus*. However, in *Tavaresia*, in early stages the outer corona consists of five discrete lobes and fusion takes place only later. In these early stages it is impossible to separate gynostegia of *Tavaresia* and, for example, *S. insignis*. The position in *Orbea* is more variable and was dealt with in detail in Bruyns (2002).

(2) Inner and outer guide rails

The presence of inner and outer guide rails in *Huernia* was first noted by Kunze (1982), and he observed this also in *Stephanotis* (of the Marsdenieae). They are also present in *Duvalia*. In *Huernia* the guide rails are seated on rather inflated cushions. These are absent in *Duvalia*, where the space behind the outer guide rail is much reduced. Further reduction is found in *Orbea*, *Tavaresia*, and *Stapelianthus*.

(3) Position of insertion crest on the pollinium

The position of the insertion crest along the edge of the pollinium in *Duvalia* and *Huernia* means that, once inserted, the pollinium lies with its flatter surface parallel to a radius from the center of the flower, and there must be sufficient room between the guide rail and the outer corona series for this to take place. This arrangement is found in several genera of the Ceropegieae (Bruyns, 2000). In the Marsdenieae, *Hoya* species with an insertion crest always have it exactly along the edge.

The condition in *Orbea*, *Stapelianthus*, and *Tavaresia*, where the insertion crest lies partly on the upper surface means that, on insertion, the pollinium will lie with its upper (flattish) surface partly turned toward the center of the flower. This allows for the development of much larger pollinia than in *Duvalia* and *Huernia*, but also for much greater restriction of the space between the outer corona and the guide rails and thus for greater involvement of the outer corona in guiding insects into the correct position for pollination. This arrangement is unique to the Ceropegieae, where the outer corona is also more developed than in any other tribe.

(4) Shape of the pollinia

The shape of the pollinia in *Orbea*, *Stapelianthus*, and *Tavaresia* is very similar and is somewhat different from that in *Duvalia* and *Huernia*.

It will usually be found that, while pollinia in *Duvalia* and *Huernia* thicken uniformly toward their center (i.e., they are more or less ellipsoidal), in *Orbea*, *Stapelianthus*, and *Tavaresia* they are thickest toward the curved part of the "D" and are significantly flattened toward the insertion crest. In this respect the pollinia of *S. pilosus* are rather unusual, and they show some similarity to "typical" *Huernia* pollinia.

(5) Shape of the top of the style head

The peculiar concave shape of the style head in *Stapelianthus* and *Tavaresia* reaches an extreme in

Tavaresia, where it is unusually thin at the center (Bruyns & Forster, 1991: fig. 7B). It is never quite as thin in *Stapelianthus* or in any other species, such as *Orbea maculata* (Bruyns, 2002), where such a construction is found. An oddity of this construction is the manner in which the parts that secrete the corpuscle may extend far above the level of the rest of the style head. Observations of early stages of the flower indicate that this is a late development, and it causes both the exposed situation of the corpuscle, the peculiar, nearly horizontal orientation of the guide rails, and the situation in some cases where the pollinia actually descend in the anther thecae.

Therefore, there are several morphological features that suggest an alliance of *Stapelianthus* with *Tavaresia*.

Molecular evidence (Figs. 4, 5). The separate analyses of the two molecular data sets (not shown) both show *Stapelianthus* as a monophyletic clade. The relationship of *Stapelianthus* with *Tavaresia*, deduced from the morphological evidence, is not supported by the molecular data, where *Tavaresia* is most closely related to *Orbea araysiana* (JK = 82). In the molecular analysis *Ballyanthus*, *Duvalia*, *Huernia*, *Orbea*, *Tridentea*, and *Tavaresia* are shown to be the most closely related genera to *Stapelianthus* among the taxa selected for the study (JK = 88). However, no well-supported close relationship of *Stapelianthus* to any of these genera was retrieved.

The evidence from the 48 informative purely molecular characters is that *Stapelianthus* occupies a distinct evolutionary line and that it is not especially closely allied to any of the African stapeliads. The relatively isolated position of *Stapelianthus* from the rest of the study group is particularly evident in the phylogram (Fig. 5) and is indicated by the long branch subtending the *Stapelianthus* clade. The many changes of characters at the base of this clade may also suggest that the genus has been isolated from the remaining taxa for a long time.

Infrageneric relationships are both poorly resolved and poorly supported. Only *Stapelianthus insignis*, *S. madagascariensis*, and *S. montagnacii* are resolved as a weakly supported clade (JK = 62) within the genus.

Combined morphological and molecular evidence (Fig. 6). When the 19 informative morphological characters are added to the two sets of molecular data, a weakly supported sister relationship between *Stapelianthus* and *Tavaresia* is formed.

Here infrageneric relationships remain both poorly resolved and poorly supported, and one finds that *S. decaryi* and *S. pilosus* are sister to the remainder of *Stapelianthus* (JK = 74). This reflects the fact that morphologically *S. arenarius*, *S. insignis*, *S. keraudreniae*, *S. madagascariensis*, and *S. montagnacii* are all quite similar, while *S. decaryi* and *S. pilosus* are more distinctive, with *S. pilosus* by far the most distinctive. In fact, *S. pilosus* has so many autapomorphies (such as the cylindrical, uniformly colored stems, the conical tubercles, and the slender leaf rudiments) that it could be said to be immediately recognizable among all of the 320 or so species of stapeliads, whether it is in flower or not. It is interesting that this is not corroborated by the molecular characters, where there is remarkably little variation among all the species of *Stapelianthus* and especially between such apparently distinctive species as *S. pilosus* and *S. arenarius*, as the phylogram (Fig. 5) demonstrates. This suggests that, whereas the genus may have been isolated for a considerable time, the few changes in molecular characters that were detected among the species may point to a more recent radiation of the species within Madagascar.

2. BIOGEOGRAPHY AND ECOLOGY

Stapelianthus is endemic to Madagascar and is the only stapeliad genus found there. The seven species grow only in the extreme south and southwest of the island from Fort Dauphin in the east to Morombe in the west (Fig. 7). These are the driest parts of Madagascar, typically receiving less than 400 mm of rain annually, though it appears that the rainfall west of Fort Dauphin (where *S. decaryi* occurs) may exceed 1000 mm in a year.

The most widely distributed species is *Stapelianthus decaryi*. This is found from near Fort Dauphin in the east northward to Ihosy and Zazafotsy on the southern edge of the central plateau and westward to Ambovombe.

The next most widely distributed species seem to be *Stapelianthus insignis* and *S. madagascariensis*. *Stapelianthus insignis* occurs from Tulear at least as far as Ejeda, Itampolo, and Ampanihy (Rauh, 1993: 36) and *S. madagascariensis* from Tulear to Ambovombe: of these two, the latter is probably the more widely distributed. *Stapelianthus pilosus* and *S. keraudreniae* appear to be rather local: the former between Ambovombe, Tsihombe, and Behara in the south and *S. keraudreniae* around Betioky in the southwest. *Stapelianthus montagnacii* occurs from Morombe southward for at least 50 km but might also occur north of Morombe, since the woodland dominated by *Didierea madagascariensis* Baillon, with which it is associated, extends northward to just south of Morondava (Rauh,

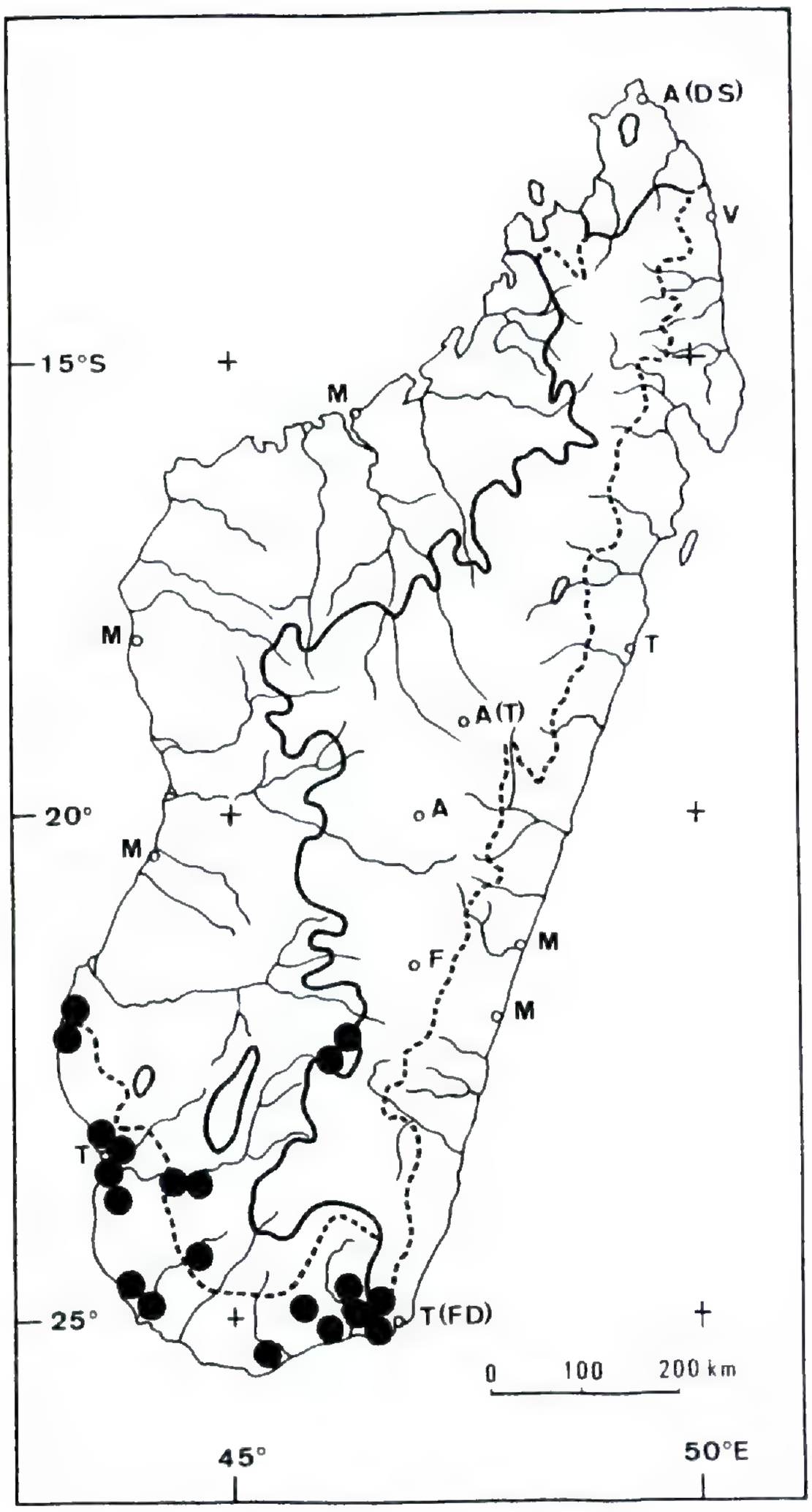

Figure 7. Distribution of *Stapelianthus*.

1978: 11). The distribution of *S. arenarius* is poorly known.

The only records of species occurring together are of *Stapelianthus madagascariensis* and *S. pilosus* around Tsihombe in the southernmost part of the island.

It would appear that most of the species are habitat-specific, and this is especially true of *Stapelianthus arenarius* and *S. insignis* in the west of the island and of *S. decaryi*, which is the only species to be found on gneiss domes. It could well be, therefore, that edaphic factors have been an important driving force behind speciation in *Stapelianthus*.

Taxonomy

Stapelianthus Choux, in A. C. White & B. Sloane, Stap., ed. 1: 71. 1933. TYPE: *Stapelianthus madagascariensis* (Choux) Choux.

Stapeliopsis Choux, Compt. Rend. Hebd. Séances Acad. Sci. Paris 193: 1444. 1931, nom. illeg., non *Stapeliopsis* Pillans, S. African Gard. 28: 32. 1928, nec *Stapeliopsis* Phillips, Fl. Pl. South Africa: t. 115. 1932. TYPE: *Stapeliopsis madagascariensis* Choux.

Small spineless non-rhizomatous succulent, forming dense to diffuse mats up to 1 m diam.; *stems* 25–200(–400) mm long, 3–15 mm thick, procumbent to decumbent, fleshy and firm, glabrous; *tubercles* arranged into 4 to 8 angles or densely covering the stem, not laterally flattened, each bearing a small leaf rudiment, which soon dries out and falls off, often bullate, without stipular denticles. *Inflorescence* glabrous, 1 per stem near base, of 1 to 3(5) flowers developing in slow succession from peduncle < 2 mm long, with 1 to 3 deltoid bracts < 1 mm long without lateral teeth; *pedicel* 3–12 mm long, 1–2 mm thick, ascending; *sepals* 2.0–9.0 mm long, subulate to lanceolate, acute. *Corolla* 10–35 mm diam., rotate to cylindrical sometimes with prominent shiny annulus; outside glabrous and smooth; inside usually with many conspicuous cylindrical obtuse papillae (very small and few only in *S. insignis*), each with a small apical bristle; *tube* usually just containing gynostegium; *lobes* usually spreading, ± deltoid, with tissue between them folded into spreading often acute lobule, margins eciliate; *corona* 2.0–6.5 mm tall, 4–8 mm broad, consisting of two series arising on staminal tube and partly intergrown, glabrous, very dark red or purple; *outer lobes* 2.5–7.5 mm long, mostly erect from base and spreading toward tips (rarely spreading from base, *S. arenarius*), free usually practically to base, forming cupular structure around central part of gynostegium and mostly much exceeding this, dorsiventrally flattened, deeply to shallowly bifid into erect to somewhat recurved narrowly deltoid lobules; *inner lobes* 0.4–1.0 mm long, adpressed to backs of anthers and rarely exceeding them, dorsiventrally flattened, small and inconspicuous, dorsally fused to cup formed by outer corona lobes; *anthers* horizontal to descending on top of style head, margins shrinking back to expose pollinia, rectangular; *pollinium* D-shaped, insertion crest twisting from outer edge to dorsal surface, caudicle attached with broad cupular pad to base. *Follicles* erect, terete-fusiform, oblavate, slender, consisting of 2 horns diverging at 30–150°, longitudinally mottled with narrow broken purple stripes, glabrous and sometimes rugulose; *seed* ± flat with cream, foam-like border and the rest pale ± brown.

Key to the Species of *Stapelianthus* in Madagascar

1a. Stems densely covered with small conical tuber-

cles, each tipped with a fine recurved hair-like leaf rudiment ..... 2. *S. pilosus*

1b. Stems distinctly 4–6(–8)-angled, tubercle tipped with a conical to narrowly deltoid leaf rudiment.

2a. Corolla with cylindrical tube; stems decumbent to erect with smooth surface ..... 1. *S. decaryi*

2b. Corolla tube not cylindrical; stems procumbent with bullate surface.

3a. Corolla ± rotate.

4a. Corolla with conspicuous shiny annulus, inside greenish to dull yellow spotted with wine- to purple-red on lobes ..... 4. *S. keraudreniae*

4b. Corolla without annulus, inside white with red-brown spots ..... 3. *S. arenarius*

3b. Corolla shallowly campanulate or bicampanulate.

5a. Corolla bicampanulate, inside smooth except for few small papillae along edges of lobes ..... 5. *S. insignis*

5b. Corolla shallowly campanulate, inside covered with conspicuous slender papillae.

6a. Corolla inside maroon to red on lobes mottled with cream in tube, outer corona lobes bifid in upper third only ..... 6. *S. montagnacii*

6b. Corolla inside cream with maroon spots, outer corona bifid at least to middle ..... 7. *S. madagascariensis*

1. Stapelianthus decaryi Choux, Ann. Inst. Bot.-Géol. Colon. Marseille ser. 5, 2(3): 7. 1934. TYPE: Southern Madagascar. Near Anosy, gneiss rocks on the eastern shore of the Ranofotsy Lagoon, July 1932, *R. Decary s.n.* (missing) (lectotype, selected here, Choux (1934: Planche IID)). Figure 8.

Stems (10–)25–100 mm long, 5–15 mm thick, forming dense clumps, decumbent to erect, gray-green to brown mottled with dark brown, surface ± smooth; *tubercles* flattened-conical, weakly joined into roughly 6(to 8) angles up stem, tapering abruptly into a narrowly conical spreading leaf rudiment 2–4 mm long and < 1 mm broad, which soon withers but persists for a time as a white nearly spine-like husk. *Pedicel* 4.0–8.5 mm long, 1.5–2.0 mm broad, ascending, holding flower facing upward; *sepals* 3–6(–7) mm long, 1.5–2.0 mm broad at base, ovate-lanceolate, acuminate, with narrow sometimes slightly recurved tips, green to cream. *Corolla* (10–)15–23 mm diam., tubular-campanulate; outside cream with fine round maroon spots; inside densely covered in upper half of tube and on lobes (becoming sparser and smaller in lower third of tube) with cylindrical papillae up to 0.6 mm long (usually with red to blackish apex) each tipped with an ascending bristle, cream with fine maroon spots usually becoming uniformly maroon on lower half of tube; *tube* (5–)10–16 mm long, 6–9 mm broad, cylindrical, usually narrowing slightly toward mouth and widest near base; *lobes* 5.0–8.5 mm long, 4–8 mm broad at base, deltoid, acute to acuminate, spreading to reflexed; *corona* 5.0–6.5 mm tall, 4–6 mm broad, dark maroon, raised on white (with few purple-red spots) pentagonal stipe up to 1.5 mm long; *outer lobes* 4.5–6.0 mm long, erect to slightly spreading, divided to middle or below into slender almost filiform slightly diverging to erect teeth, sometimes with a further small tooth between them; *inner lobes* ± 0.6 mm long, deltoid, obtuse, but not usually exceeding anthers. *Follicles* fusiform, erect, diverging at 20–30° from one another, surface smooth and mottled with longitudinal purple lines on a cream background; *seed* variable in size, 5.0–6.0 × 2.5–4.0 mm, elliptic to nearly circular, border rather inflated, whole seed pale brown or yellow-brown.

Distribution. Widely distributed in southern Madagascar. Elevation 10–900 m.

Ecology. *Stapelianthus decaryi* mainly inhabits pockets of soil or leaf litter on gneiss domes along the foot and lower slopes of hills. Plants are generally found growing entirely in the open, without any protection. Around Fort Dauphin it is common and grows in the company mainly of *Pachypodium horombense* H. Poiss., *Kalanchoe orgyalis* Bak., and *Ischnolepis graminifolia* (Costantin & Gallaud) Klack. Around Ihosy the habitat is very similar, and here it grows with *Pachypodium rosulatum, Kalanchoe orgyalis,* and *Euphorbia xylophylloides* A. Brogn. ex Lem. among a host of other succulents. Near Zazafotsy it was observed on flat, gneiss outcrops covered scantily with *Xerophyta, Aloe intermedia* (H. Perr.) Reynolds, and *Kalanchoe synsepala* Bak.

Discussion. *Stapelianthus decaryi* is most easily recognized when sterile by its almost erect stems clustered together into densely packed clumps (which may be up to 1 m diam.) with their almost spine-like leaf rudiments. The tubular flowers covered densely inside with short, conical papillae are also distinctive. The flowers are extremely variable, and some with tubes as short as 5 mm were observed near Ihosy.

In *Stapelianthus decaryi* several follicles have been seen, and they have been found to contain variable numbers of seeds: 35 seeds were counted in one solitary follicle, 76 in another pair, 52 in another pair, and 12 in a further very small pair.

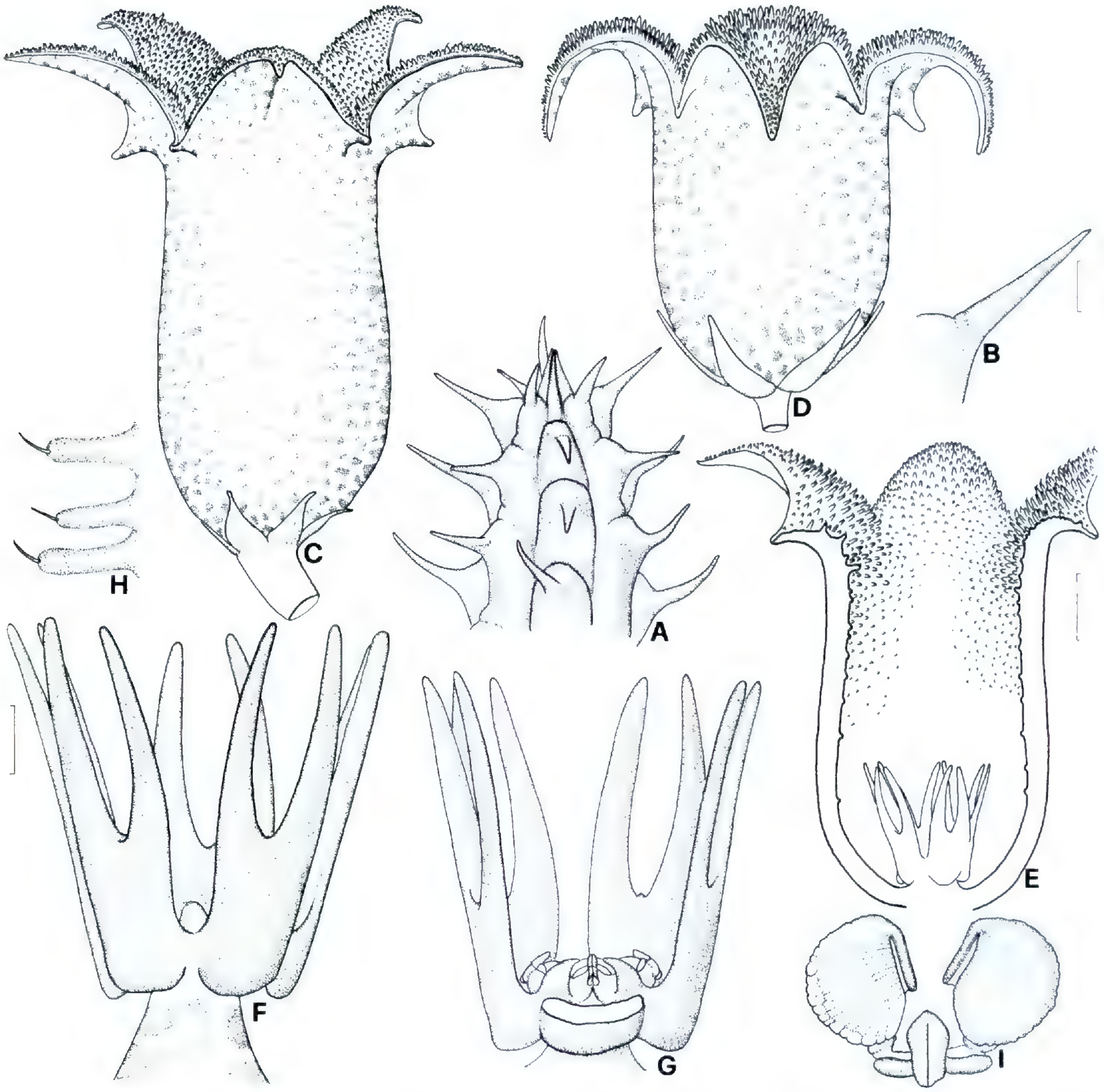

Figure 8. *Stapelianthus decaryi*.—A. Portion of stem. —B. Leaf rudiment. —C, D. Side view of flower. —E. side view of dissected flower. —F. Side view of gynostegium with tall basal stipe. —G. Side view of gynostegium with one outer corona lobe removed and with much shorter stipe. —H. Papillae inside corolla around mouth of tube. —I. Pollinarium. Scale bars: A, C–E, 3 mm (at E); B, 1 mm; F, G, 1 mm (at F); H, 0.5 mm (at F); I, 0.25 mm (at F). Drawn from A–C, E, G, *hort. de Boer*; D, H, *hort. Oxford*; F, I, *PVB 5960*.

The type of *Stapelianthus decaryi* is missing. One of the illustrations published with the protologue is selected as a lectotype, since this clearly illustrates both the shape and habit of the stems and the shape of the corolla and thus characterizes the species clearly.

Specimens examined. MADAGASCAR. N of Zazafotsy, *Bruyns 6191* (BOL); Zazafotsy escarpment, 22 July 1958, *Descoings 3794* (TAN); Fort Dauphin, *Descoings 3759* (TAN); 8 km W of Ihosy, *Bruyns 6216* (BOL); valley of Manambolo, near Esomony, 400–900 m, Dec. 1933, *Humbert 13160* (P); 50 km W of Fort Dauphin, *Hardy 2894* (PRE); Ambovombe, 9 Jan. 1933, *Decary* (K, TAN); Manambaro, *Bruyns 5960* (BOL); Andohahela, near Hazofoty, 6 Feb. 1989, *Du Puy et al. 19877* (TAN); Andohahela, Parcelle 2, 125 m, *Phillipson 2922* (K, P); near Italy, *Descoings 2669* (P), *Du Puy et al. M 838* (K); Berenty Reserve, *Lucille 948* (P); Ranopiso, *Decary 10721* (P); near Ihosy, *Bosser 19684* (P); Andrahomana, *Decary 3114* (P).

2. Stapelianthus pilosus Lavranos & D. S. Hardy, J. S. African Bot. 27: 237. 1961. *Trichocaulon decaryi* Choux, Ann. Inst. Bot.-Géol. Colon. Marseille ser. 4, 10: 6, 10. 1932. TYPE: Southern Madagascar. Mount Angavo, 1 Apr. 1931, *R. Decary 8820* (lectotype, selected here, P!; isotypes, K!, TAN!). Figure 9.

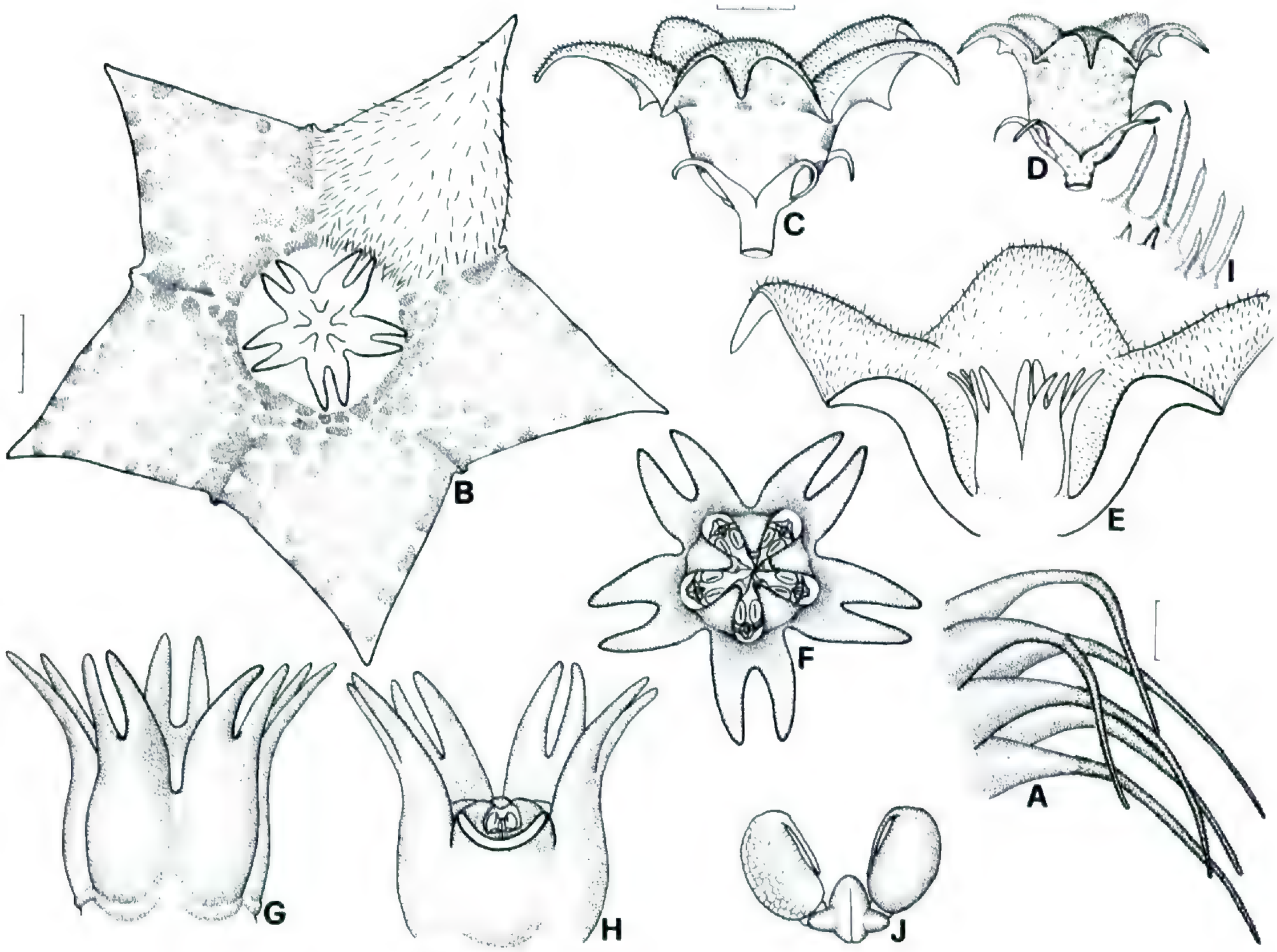

Figure 9. *Stapelianthus pilosus*.—A. Tubercles on stem. —B. Face view of flower. —C, D. Side view of flower. —E. Side view of dissected flower. —F. Face view of gynostegium. —G. Side view of gynostegium. —H. Side view of gynostegium with one outer corona lobe removed. —I. Papillae inside corolla near base of lobes. —J. Pollinarium. Scale bars: A, 1 mm; B, E, 2 mm (at B); C, D, 3 mm (at C); F–H, 1 mm (at C); I, 0.5 mm (at C); J, 0.25 mm (at C). Drawn from A, D, I, J, *PVB 5959*; rest, *hort. de Boer*.

Stems 30–300 mm long, 8–12 mm thick, decumbent (rarely procumbent), green (purplish when exposed), smooth, ± cylindrical, covered densely with conical tubercles each tipped with a filiform leaf rudiment 2.5–6.0 mm long, leaf rudiment rapidly drying out to a persistent recurved whitish hair. *Pedicel* 3–7 mm long, 1.0–1.5 mm thick, ascending, holding flower facing at least partly upward, green sometimes speckled with purple and sometimes with scattered papillae toward apex; *sepals* 3.0–4.5 mm long, 1.0–1.5(–2) mm broad at base, subulate, acuminate-filiform usually curling backward toward apex, green sometimes speckled with purple, smooth. *Corolla* 10–18 mm diam., campanulate; outside cream spotted with maroon; inside covered with slender columnar papillae 0.50–0.75 mm long each with a sharp apical bristle, cream to pale yellow spotted with dark purple; *tube* 3–4 mm long, cupular; *lobes* 3.5–7.0 mm long, 4–6(–9?) mm broad at base, deltoid, usually spreading with apices somewhat recurved; *corona* 3.5–4.0 mm tall, 2.5–3.0 mm broad, dark maroon, seated on short stipe; *outer lobes* 2.4–3.5 mm long, fused for nearly half length of gynostegium, erect with spreading apices, convex outside and somewhat concave within, deeply bifid into ± parallel narrowly lanceolate acute lobules; *inner lobes* ± 0.4 mm long, deltoid, obtuse, usually not exceeding anthers.

Distribution. Southern Madagascar, between Tulear and Behara. Elevation 1–500 m.

Ecology. *Stapelianthus pilosus* may grow among small bushes in denuded areas or even in exposed places on rocks. However, it appears to prefer dry, xerophytic forests, where plants thrive in accumulations of leaf litter on the floor of the forest.

Discussion. Choux described this as *Trichocaulon decaryi* because of its very unusual stems. Within *Stapelianthus*, where the inflorescence, flowers, and especially the corona suggest it belongs, it occupies a rather isolated position morphologically. In the other species of the genus the surface of the stem is bullate, marked with dark patches on a pale background; here it is smooth

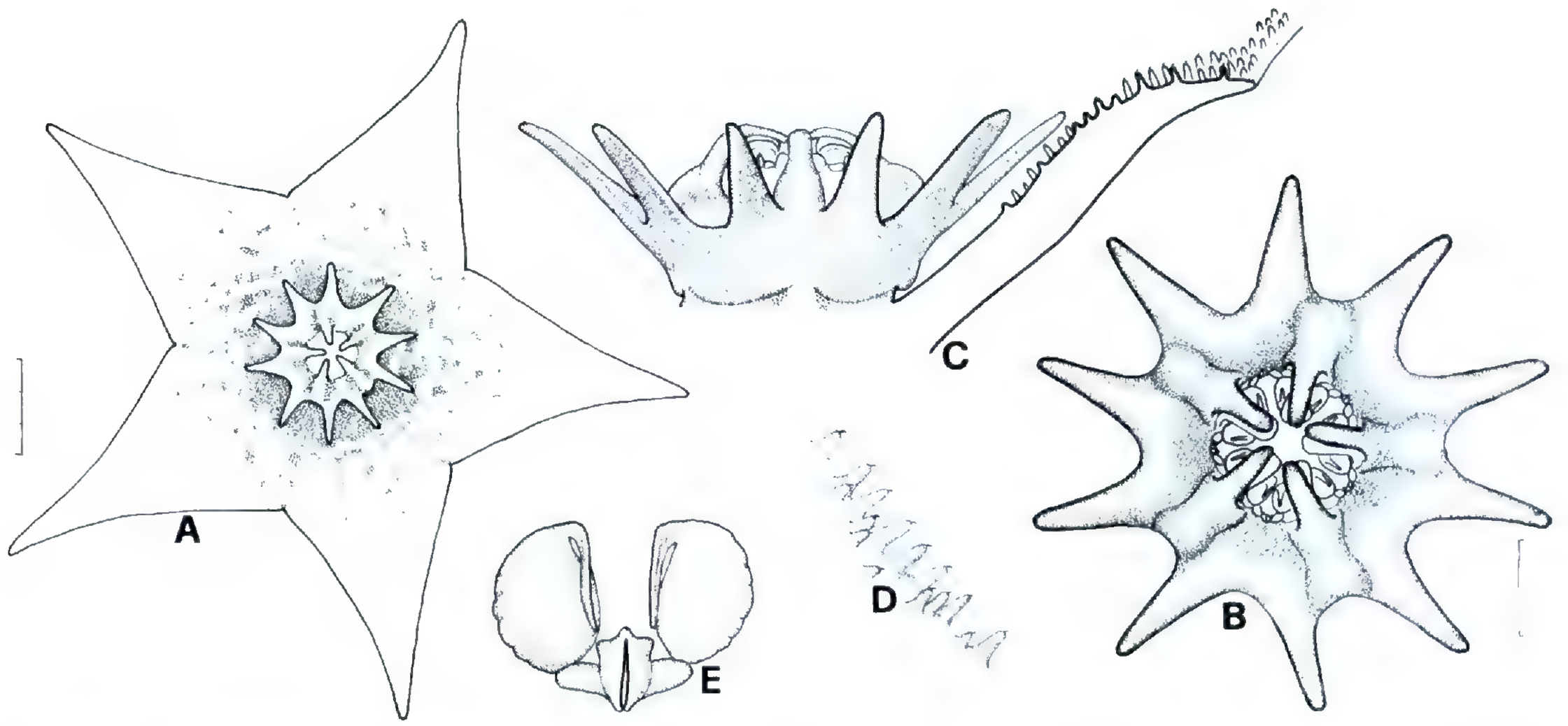

Figure 10. *Stapelianthus arenarius.*—A. Face view of flower. —B. Face view of gynostegium. —C. Side view of gynostegium with part of corolla tube. —D. Papillae inside corolla near base of lobes. —E. Pollinarium. Scale bars: A, 3 mm; B, C, 1 mm (at B); D, 0.5 mm (at B); E, 0.25 mm (at B). Drawn from *PVB 5954.*

and uniformly green (if sheltered). The sepals are unusually long and slender relative to the size of the flower. The corona is also unusual in that the outer lobes are fused into a cup to just below their middle. The pollinaria are particularly small with a disproportionately large corpuscle, nearly ellipsoidal pollinia, and short wings on the corpuscle.

Material at P indicates that Decary discovered this species at Mount Kokomba in January of 1918. Choux (1932: 10) provided a Latin diagnosis of this species but did not mention a type specimen with it. However, on page 6 he mentioned two collections, namely *Decary 8820* from Mount Angavo and *Decary 9033* from between Behara and Tranomaro. *Decary 8820* is at K, P, and TAN, while *Decary 9033* has only been located at BM. Since it is more widely distributed, I have selected *Decary 8820* as the lectotype.

Specimens examined. MADAGASCAR. Angavo, *Rauh 9462* (PRE), *Decary 4549* (PRE); between Behara and Tranomaro, *Decary 9033* (BM); 12 km N of Behara, *Hardy 2936* (PRE); Mt. Kokomba, 180 m, *Decary s.n.* (P); Tsihombe, *Bruyns 5959* (BOL); 2–3 km N of Behara, *Von Arx & Supthut BVA 30* (TAN); N side of Onilahy Estuary, 1–150 m, *Humbert & Capuron 29541* (P).

3. Stapelianthus arenarius Bosser & Morat, Adansonia N.S., 11: 340–341. 1971. TYPE: Western Madagascar. Route to Manombo N of Tulear, *J. Bosser & P. Morat 20392* (holotype, P not seen). Figure 10.

Stapelianthus calcarophilus Morat, Bull. Mus. Natl. Hist. Nat., B, Adansonia, 12: 3. 1990. Syn. nov. TYPE: South Madagascar. Itampolo, 12 Apr. 1972, *P. Morat 3973* (holotype, P not seen).

Stems 50–150 mm long, 5–10 mm thick, procumbent often with apices ascending, gray-green marked with purple-brown, surface bullate; *tubercles* arranged roughly into 4 rows, tipped with a small narrowly lanceolate recurved leaf rudiment 1–2 mm long and 0.5 mm broad, slightly flattened above. *Pedicels* 3–10 mm long, 1.0–1.5 mm thick, erect, holding flower facing upward, pinkish green; *sepals* 2.0–4.0 mm long, 1.5 mm broad at base, lanceolate-acute, whitish. *Corolla* 20–25 mm diam., ± rotate; outside dull white finely dotted with pale maroon; inside finely papillate over whole surface except base (papillae up to 0.3 mm tall), white with few maroon spots toward base, tube white spotted with maroon coalescing behind corona; *tube* ± 2 mm deep, very broad and shallow, containing gynostegium; *lobes* 8–13 mm long, 4.5–5.5 mm broad at base, deltoid-acute, spreading to recurved; *corona* 2 mm tall, 4–5 mm broad, maroon-black, seated on very short stipe; *outer lobes* 2.5–2.8 mm tall, free practically to base, bifid to below level of inner lobes into slightly ascending-spreading narrowly obtuse teeth; *inner lobes* 0.7–1.0 mm long, linear oblong, ± adpressed to and equaling anthers. *Follicles* fusiform, with fairly slender horns (3–4 mm thick at max.) diverging at ± 150°, surface covered with irregular ridges and mottled with purple on a paler background; *seed* 6.9–6.5 × 3.0 mm, pear-shaped, slightly raised pale border, rest pale pinkish brown.

Distribution. Southwestern Madagascar. Elevation 10–100 m.

Ecology. *Stapelianthus arenarius* grows in fine,

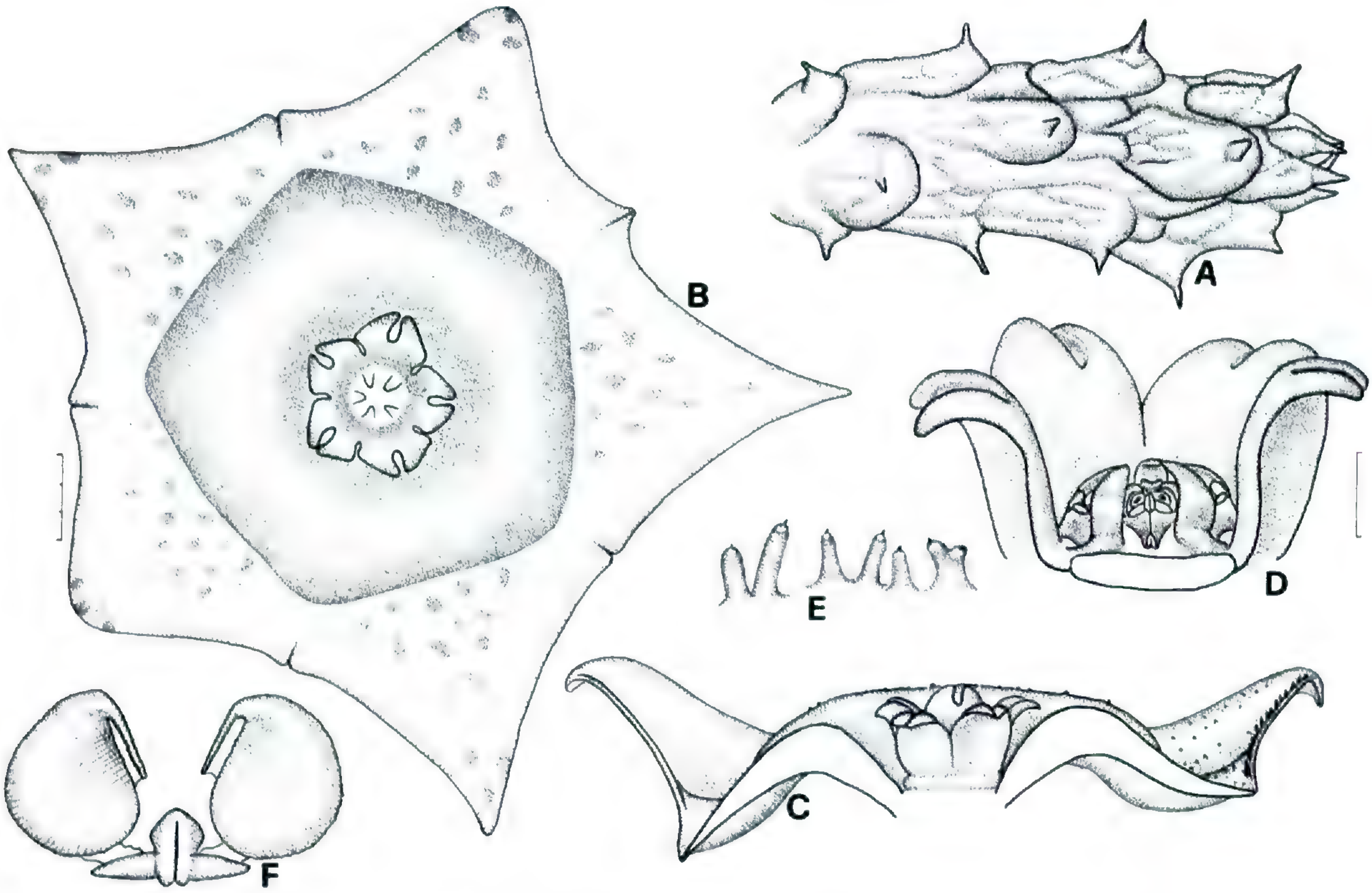

Figure 11. *Stapelianthus keraudreniae.*—A. Portion of stem. —B. Face view of flower. —C. Side view of dissected flower. —D. Side view of gynostegium with one outer corona lobe removed. —E. Papillae inside corolla along edges of lobes. —F. Pollinarium. Scale bars: A–C, 3 mm (at B); D, 1 mm; E, 0.5 mm (at D); F, 0.25 mm (at D). Drawn from *hort. J. H. v. d. Merwe.*

deep, red sand within 1 km of the sea in *Didierea madagascariensis* forest north of Tulear, where plants are common among leaf litter under bushes and trees. Their wrinkled surface lends them an extraordinary resemblance to dried twigs: when very dry they become prostrate and partly hidden among dried leaves and practically invisible, when in better condition rising up out of the leaf-litter and becoming much more visible.

Discussion. This species has unusual flowers: they are nearly flat with white corolla lobes (sometimes faintly brownish) becoming spotted with maroon toward the center. The stems are paler, much more rugulose than those of other *Stapelianthus* species, with very slender leaves, and they are not clearly 4-angled especially when in a dry state. The rugose follicles are unique in the genus and among all the stapeliads.

There seem to be no obvious reasons not to include *Stapelianthus calcarophilus* under *S. arenarius.* In *S. calcarophilus* the sepals and flowers are slightly smaller and the corolla lobes are reflexed. These differences are minor indeed and seem to be outweighed by the similarity between them in the shape of the flower and its coloring as well as in the shape and also the orientation of the outer corona lobes. I can find no reason not to reduce *S. calcarophilus* to synonymy.

Specimen examined. MADAGASCAR. N of Tulear, Ifaty, *Bruyns 5954* (K).

4. Stapelianthus keraudreniae Bosser & Morat, Adansonia, N.S., 11: 337, 339. 1971. TYPE: Southwestern Madagascar. Betioky district, Ankazoabo gorge, *J. Bosser & P. Morat 19413* (holotype, P not seen). Figure 11.

Stems 25–150(–400) mm long, 4–10 mm thick, forming dense to diffuse clumps, procumbent or with erect apices, purple-brown flecked on gray-green background, surface bullate; *tubercles* broadly flattened-conical, weakly joined into 4 or 5(to 7) angles along stem, tapering abruptly into small, narrowly lanceolate, recurved leaf rudiment 1–2 mm long, which is somewhat flattened above and gradually withers and falls off. *Pedicel* 3–7 mm long, 1.5 mm thick, ascending to erect holding flower facing upward; *sepals* 3–7 mm long, 1.5–2.0 mm broad at base, ovate-lanceolate, acute, green suffused faintly with purple. *Corolla* 20–35 mm diam., ± rotate; outside pale green finely spotted with red to brown (often arranged in "veins"), with 3 to 5

raised longitudinal veins on each lobe, smooth; inside with scattered small obtusely conical usually purple-tipped papillae becoming longest (up to 0.3 mm long) and densest along edges of lobes and in mouth of tube but absent on outer side of annulus (sometimes only along margins of lobes), each tipped with small apical and often obtuse bristle, annulus somewhat shiny, pale red to dark purple-red or densely spotted with red-purple, lobes greenish to dull yellow spotted with wine- to purple-red; *tube* ± 3 mm long, 6–8 mm broad, pentagonal, broadly V-shaped, just containing gynostegium, thickened into cushion-like raised circular annulus around mouth; *lobes* 7–10 mm long, 8–12 mm broad at base, ascending to spreading or recurved, ovate, acute, usually with reflexed tips; *corona* 3.0–4.5 mm tall, 5–6 mm broad, red to dark maroon, shiny, seated on very short stipe; *outer lobes* 3.0–4.5 mm long, 2–3 mm broad, erect, spreading above close to mouth of tube, slightly concave outside and convex within, bifid in upper quarter to third into obtuse spreading to reflexed lobules; *inner lobes* ± 0.6 mm long, shorter than anthers, oblong-linear. *Seed* 5.0 × 2.5 mm, pear-shaped, swollen pale border, rest pale brown.

Distribution. Southwestern Madagascar. Elevation 50–320 m.

Ecology. *Stapelianthus keraudreniae* is known from areas apparently underlain by sandstones (Rauh, 1998), where the plants grow in the shelter of small bushes.

Discussion. The flowers of *Stapelianthus keraudreniae* are quite remarkably reminiscent of those of, say, *Huernia zebrina* (except for being much smaller) and are very pretty. As usual, there is considerable variation in color, particularly from dark to pale red, and the conspicuous, shiny annulus may be spotted or uniformly red. The flowers emit a faint bad odor of excrement, and some drops of nectar-like secretion are sometimes found on the annulus.

Specimens examined. MADAGASCAR. SE of Tulear, near Beza Mahafaly, *P.R. Alp s.n.* (BOL); Beza Mahafaly, 18 Apr. 1987, *Phillipson 1674* (TAN).

5. Stapelianthus insignis Desc., Naturaliste Malgache 9: 181–182. 1957. TYPE: Southwestern Madagascar. 21–23 km from Tulear toward Tongobory near the Onilahy River, *B. Descoings 2751* (TAN missing) (lectotype, selected here, Descoings (1957: fig. 1a–f)). Figure 12.

Stapelianthus insignis subsp. *tongoboryensis* Rauh, Trop. Subtrop. Pflanzenwelt 85: 36. 1993. Syn. nov. TYPE: In deciduous forests near Tongobory, *W. Rauh 21874* (holotype, HEID not seen).

Stems 50–200 mm long, 5–12 mm thick, procumbent to decumbent, often with apices ascending, (red-)gray- to cream-green marked with purple-brown, surface bullate; *tubercles* broad and flattened, somewhat joined into 4(or 5) rows along stem so that stem is ± square in cross section, tapering abruptly into small, narrowly lanceolate, spreading to recurved leaf rudiment 1–2 mm long, which is slightly flattened above, gradually withering and falling off. *Pedicel* 4–8 mm long, 1–2 mm thick, ascending-erect and holding flower facing ± upward, sometimes longitudinally grooved, purplish; *sepals* 5–8 mm long, 2–3 mm broad at base, subulate with narrow, slightly recurved apex, smooth. *Corolla* 17–26 mm diam. at max., bicampanulate; outside pale green finely to boldly speckled with purple; inside smooth except for few small papillae along edge of corolla lobes, boldly speckled with purple on pale yellow-green; *tube* 5–10 mm long, 6–7 mm broad, cupular, fabric noticeably thickened at mouth beyond which corolla widens to maximum and then constricts to variable but sometimes very narrow pentagonal mouth (6–16 mm diam.); *lobes* ± 2–3 mm long, 3–10 mm broad at base, broadly and shortly triangular, acute, usually recurved; *corona* 4.5–6.0 mm tall, 4–6 mm broad, dark maroon, seated on short stipe; *outer lobes* 4.0–7.5 mm long, free practically to base, erect to slightly spreading, concave outside and with slight medial groove inside, deeply to only shallowly bifid into ± parallel lobules; *inner lobes* ± 0.6 mm long, deltoid, obtuse, not usually exceeding anthers. *Seed* 5 × 3 mm, broadly pear-shaped, very swollen border paler than rest.

Distribution. Southwestern Madagascar. *Stapelianthus insignis* is widely distributed, occurring from the limestone hills just east of Tulear (and possibly further north as well) southward to Ejeda and Ampanihy (Rauh, 1993: 36). Elevation 20–300 m.

Ecology. *Stapelianthus insignis* occurs in flat areas or on the lower slopes of hills. It always seems to grow among pieces of limestone and small bushes (very often a small, spiky member of the Asteraceae) along the edges of denser bush.

Discussion. The flowers seem to be extremely variable in color and also in the degree to which they close up toward the mouth. Descoings's original material was practically plain pale green outside with a very narrow mouth to the flower (± 6 mm diam.). Some subsequent collections have had a boldly spotted corolla (outside) with much broader opening (up to 16 mm diam.). However, the type

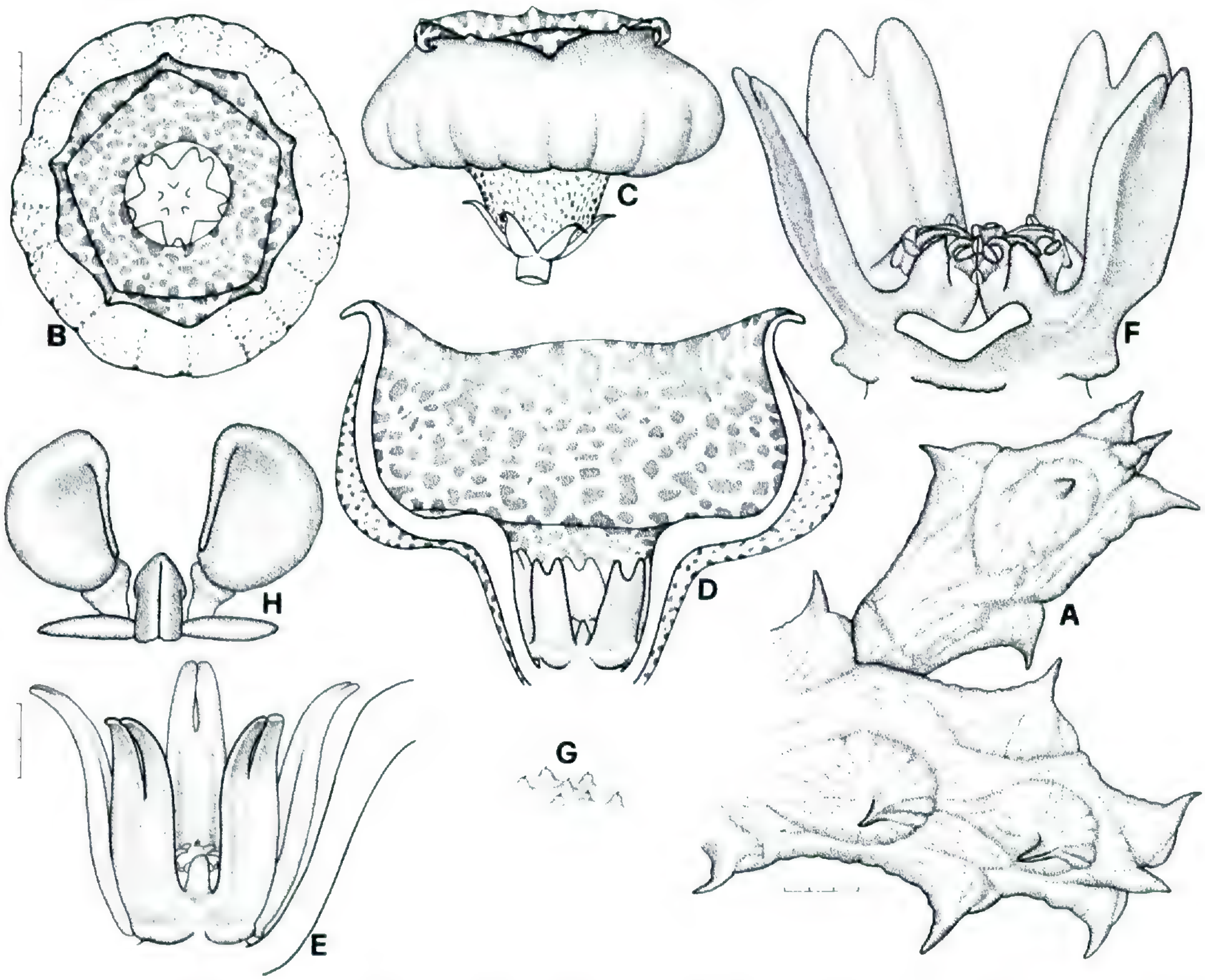

Figure 12. *Stapelianthus insignis.*—A. Portion of stem. —B. Face view of flower. —C. Side view of flower. —D. Side view of dissected flower. —E. Side view of gynostegium. —F Side view of gynostegium with one outer corona lobe removed. —G. Papillae inside corolla along edges of lobes. —H. Pollinarium. Scale bars: A, D, 3 mm (at A); B, C, 5 mm (at B); E, 2 mm; F, 1 mm (at E); G, 0.5 mm (at E); H, 0.25 mm (at E). Drawn from A, E, G, H, *PVB 6208*; rest, *hort. de Boer.*

plant of Descoings came from the same area as the newly described subspecies of Rauh (i.e., Tongobory, near the Onilahy River) so that there is no reason to believe that two geographically discrete color forms are involved. In addition, flowers with darkly and boldly mottled exteriors have also been found near La Table east of Tulear. It would be more reasonable to consider them all as variants of a single species, and, consequently, *Stapelianthus insignis* subsp. *tongoboryensis* is not recognized.

The buds of this species remain more or less cylindrical until they are about 8 mm long, after which the upper part begins to swell outward somewhat below the bases of the corolla lobes. This outward swelling ultimately gives the corolla its bicampanulate shape and produces a bud with a roughly flat upper surface with the folds at the sinuses of the lobes projecting from this surface quite close to its center and pointing in the direction of the center. This is a most unusual arrangement: in species with an annulus, such as *Stapelianthus keraudreniae* and various Huernias, these projecting folds always remain beneath or at the edge of the flat upper area in the bud. In other words, the expansion of the upper part of the corolla keeps up with that of the lower: in *S. insignis* the lobes remain quite short so that the expansion of the lower part of the corolla outpaces that of the lobes and leaves them behind near the center of the bud.

The flowers appear to be odorless.

I have been unable to locate any material of the type. This collection was illustrated in great detail by Descoings, and so these illustrations are selected as a lectotype.

Specimens examined. MADAGASCAR. Near Tulear, coastal limestone, *Hardy & Rauh 2795* (PRE); 20 km E of Tulear, *Bruyns 6194 a* (K); La Table, E of Tulear, *Bruyns 5933* (BOL); St Augustin, *Bruyns 6208* (E). Betioky, *Bruyns 5956* (PRE); Tongobory, *Bruyns 5955* (MO). Ejeda, *Bruyns 5957* (BOL).

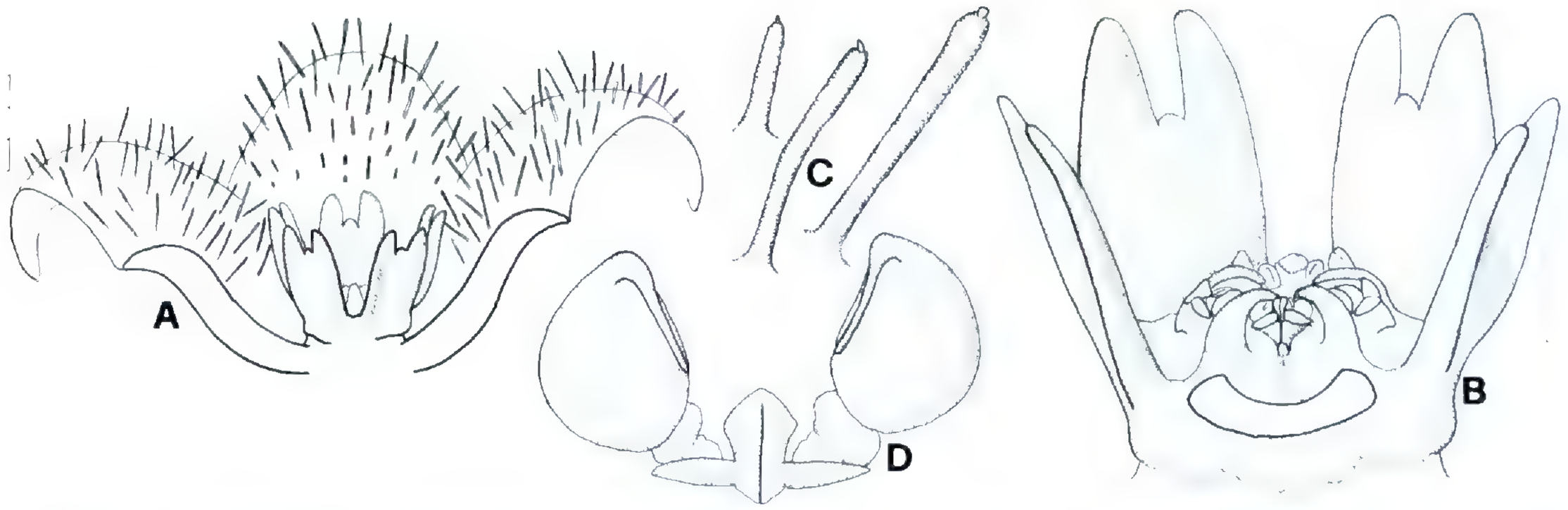

Figure 13. *Stapelianthus montagnacii*.—A. Side view of dissected flower. —B. Side view of gynostegium with one outer corona lobe removed. —C. Papillae inside corolla near base of lobes. —D. Pollinarium. Scale bars: A, 3 mm; B, 1 mm; C, 0.5 mm (at B); D, 0.25 mm (at B). Drawn from *hort. de Boer*.

6. Stapelianthus montagnacii (Boiteau) Boiteau & Jean Bertrand, Cactus (Paris) 26: 116. 1950. *Stapelia montagnacii* Boiteau, Bull. Trimestriel Acad. Malgache, N.S. 24: 83. 1942. TYPE: Southwestern Madagascar. Near Tulear, Dec. 1941 (fl), *P. Montagnac sub Jardin Bot. Tananarive 4938* (TAN missing) (lectotype, selected here, Cactus (Paris) 26: 116, photo by G. Richard, 1950). Figures 13, 14, 15.

Stapelianthus hardyi Lavranos, Natl. Cact. Succ. J. 26: 67. 1971. Syn. nov. TYPE: Western Madagascar. Near Morombe, 12 Apr. 1971, *D. S. Hardy & Jacobsen 3569* (holotype, P not seen; isotypes, FT not seen, K not seen, PRE!).

Stems 25–300 mm long, 6–10(–15) mm thick, procumbent often with ascending apices, mottled with green to purplish on gray to cream background, surface bullate; *tubercles* broad and flattened to conical, weakly joined into 4(to 6) angles along stem, tapering abruptly into small, narrowly lanceolate, recurved leaf rudiment 1–2 mm long, grooved above leaf rudiment, leaf rudiment slightly

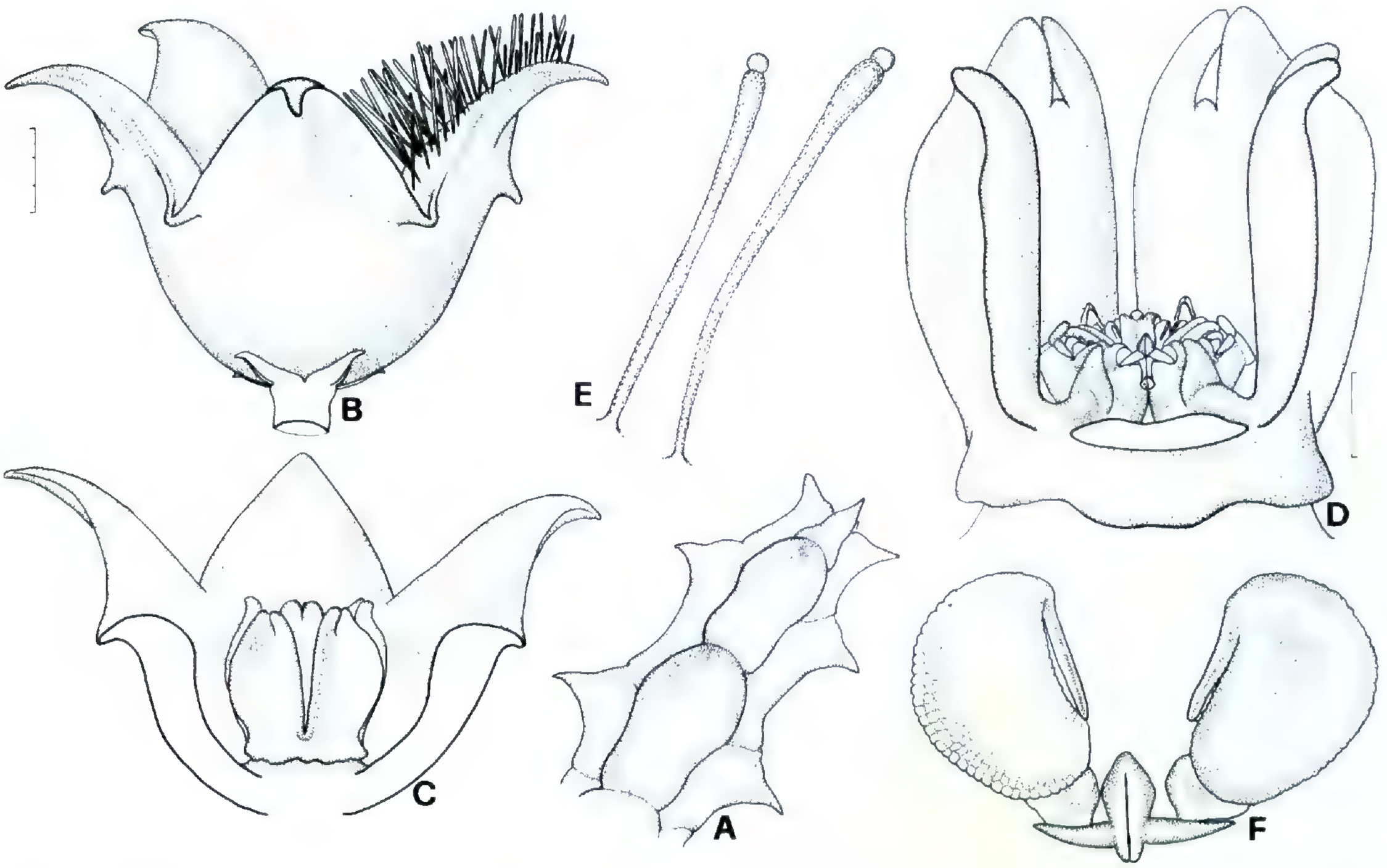

Figure 14. *Stapelianthus montagnacii*. Material formerly known as *S. hardyi*.—A. Portion of stem. —B. Side view of flower. —C. Side view of dissected flower. —D. Side view of gynostegium with one outer corona lobe removed. —E. Papillae inside corolla near base of lobes. —F. Pollinarium. Scale bars: A–C, 3 mm (at B); D, 1 mm; E, 0.5 mm (at D); F, 0.25 mm (at D). Drawn from *PVB 6200*.

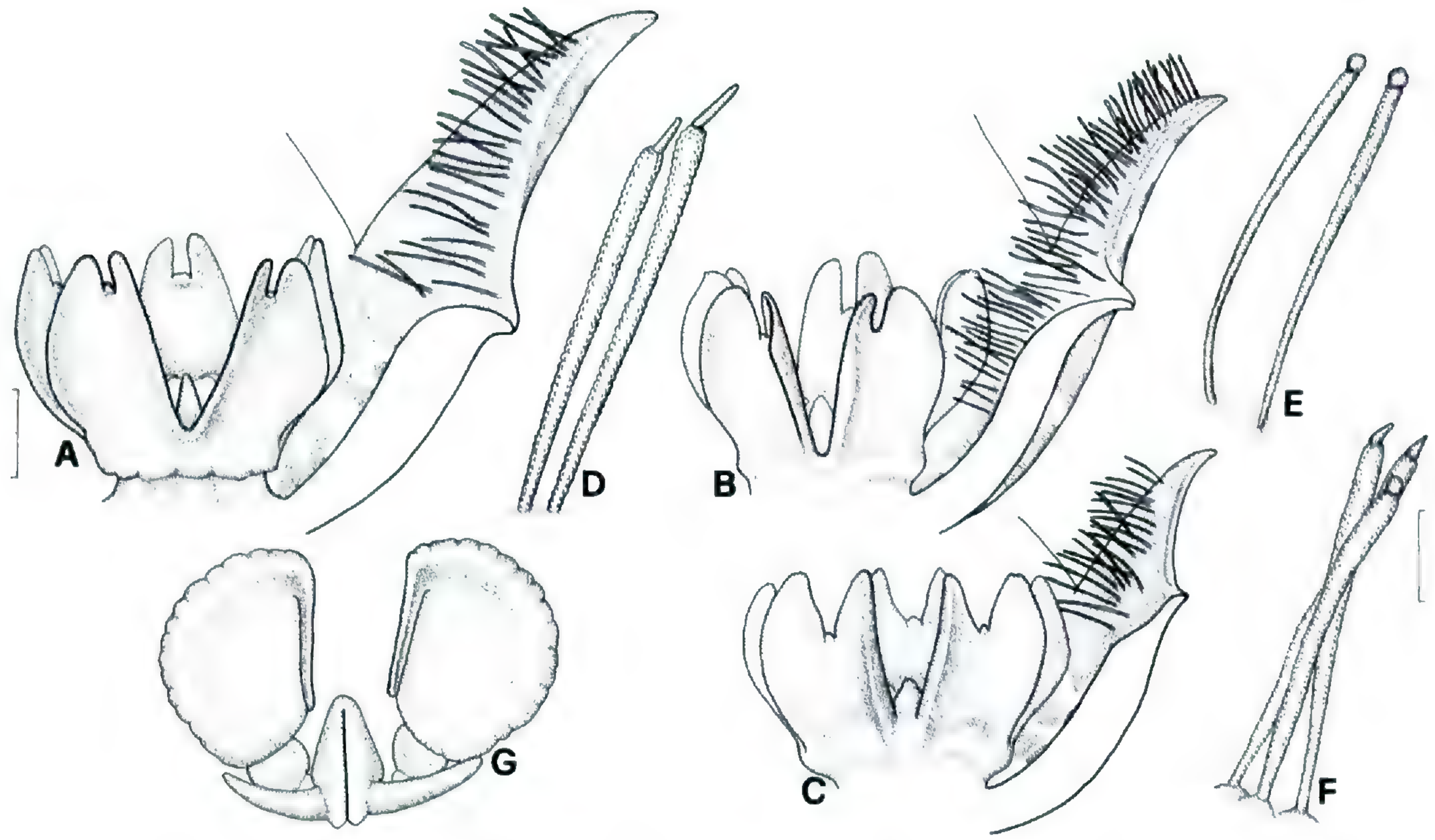

Figure 15. Intermediates between *Stapelianthus montagnacii* and the former *S. hardyi* [= *S. montagnacii*]. —A–C. Side view of center of dissected flower. —D–F. Papillae inside corolla along edges of lobes. —G. Pollinarium. Scale bars: A–C, 2 mm (at A); D–F, 0.5 mm (at F); G, 0.25 mm (at F). Drawn from A, D, G, *PVB 6203* (similar to *S. hardyi* but corolla tube more mottled, outer corona lobes shorter, and papillae with elongated apical bristle); B, C, E, F, *PVB 6195* (mixed population with smaller flowers more like typical *S. montagnacii*, papillae with variable apical bristles).

flattened above and gradually withering and falling off. *Pedicel* 7–12 mm long, 2.0–2.5 mm thick, spreading and holding flower facing horizontally; *sepals* 2.5–3.0 mm long, 1.5 mm broad at base, ovate-triangular, acute, smooth, with recurved apices. *Corolla* (13–)20–30 mm diam., shallowly campanulate; outside maroon becoming cream with maroon to red spots toward apex of lobes and base; inside densely covered (in maroon portion except at tips of lobes) with slender cylindrical maroon papillae up to 3 mm long usually slightly thickened toward apex and with spherical apical "bristle," maroon to red on lobes and onto mouth of tube, below this cream concentrically speckled with maroon to red becoming plain cream in base of tube; *tube* 4–10 mm long, 9–17 mm broad, somewhat thickened around mouth; *lobes* 6–9 mm long, 6–9 mm broad at base, deltoid, acute to acuminate, erect to spreading; *corona* 4–6 mm tall, 6–8 mm broad, dark red, seated on short stipe; *outer lobes* 4–5 mm long, free practically to base, erect, concave outside and convex inside with groove down middle, rather variably bifid in upper third into erect deltoid lobules often with a smaller third one between them; *inner lobes* ± 0.5 mm long, ± deltoid, much shorter than to equaling anthers. *Follicles* fusiform, with fairly stout horns diverging at ± 150°, surface smooth, mottled with longitudinal purple lines on a gray background; *seed* 5–7 × 2.5–4.0 mm, pear-shaped, swollen pale-brown border, rest darker brown.

Distribution. Southwestern Madagascar, from southeast of Tulear to Morombe. Elevation 10–200 m.

Ecology. Stapelianthus montagnacii always seems to occur in flat areas. Habitats vary from fine sand in *Didierea madagascariensis* bush, to among thick leaf litter on the floor of *Euphorbia tirucalli* L.–*E. intisy* Drake thickets growing on loam. Plants have also been seen in small pockets of soil on limestone outcrops between stones and small bushes.

Discussion. There seems to have been some uncertainty expressed in the literature about the distinctness of *Stapelianthus madagascariensis* and *S. montagnacii*. Rauh (1963: 148) listed all the differences that he could find between them. These amounted to the slightly thicker stems (6–10 mm thick) in *S. montagnacii* (as opposed to 3–9 mm thick in *S. madagascariensis*), the slightly longer corolla lobes in *S. montagnacii* (the lobes measured 7–8 mm long and 7 mm broad in *S. madagascariensis*, 6 mm long and 6 mm broad in *S. montagnacii*), the darker-colored corolla in *S. montagnacii*, and the outer corona lobes that are only bifid in the upper third in *S. montagnacii* (divided to the middle in *S. madagascariensis*). He concluded that only one species was probably involved. Rauh

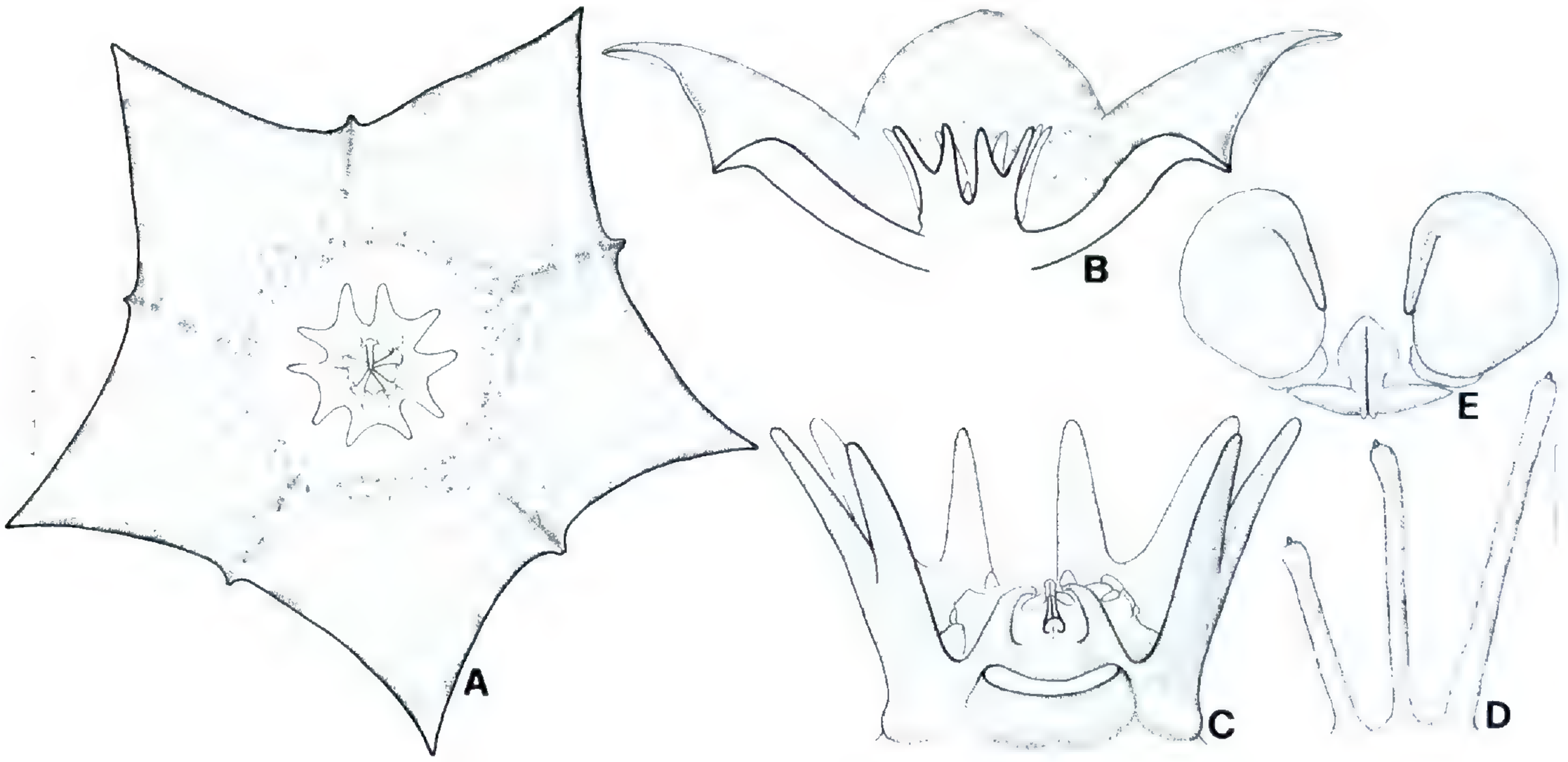

Figure 16. *Stapelianthus madagascariensis.*—A Face view of flower. —B. Side view of dissected flower. —C. Side view of gynostegium with one outer corona lobe removed. —D. Papillae inside corolla around mouth of corolla tube. —E. Pollinarium. Scale bars: A, B, 3 mm (at A); C, 1 mm (at D); D, 0.5 mm; E, 0.25 mm (at D). Drawn from *PVB 5958.*

(1963: 148) mentioned also that *S. montagnacii* is more difficult to cultivate than *S. madagascariensis*, but this is a characteristic that is difficult to interpret taxonomically, though it may be related to the different edaphic conditions from which the plants originated.

Later, Rauh (1998) also suggested that *Stapelianthus hardyi* cannot be clearly separated from *S. madagascariensis*. However, the real problem with *S. hardyi* is that it is not possible to separate it from *S. montagnacii*. *Stapelianthus hardyi* shares with *S. montagnacii* the slightly thicker stems, the darker color of the corolla, and the outer corona lobes that are only bifid in their upper third. The main differences between them lie in the somewhat darker, more deeply bowl-shaped flower of *S. hardyi*, its slightly thicker corolla, the longer papillae on the corolla with spherical apical "bristle," the rather more massive outer corona lobes, and the larger pollinia. However, material gathered some 30 km north of Tulear (*PVB 6195*) is intermediate between the two in many respects. Here the flower is not quite so dark and inside the mottling of maroon on cream may continue right to the mouth of the tube, the tube is shallower (at only 4–6 mm deep), and the pollinia are smaller. For the present it would seem that the most suitable arrangement is to place *S. hardyi* and *S. montagnacii* together.

The type of this species is missing. A lectotype is selected, using the illustration published by Boiteau and Bertrand (1950: 116). Although this is not explicitly stated as being of *Montagnac 4938*, it is assumed here that this photograph is of the material on which Boiteau based his original description.

Specimens examined. MADAGASCAR. 2 km S of Morombe, *Bruyns 6200* (MO); 40 km S of Morombe, *Bruyns 6203* (BOL); 30 km N of Tulear, *Bruyns 6195* (BOL).

7. Stapelianthus madagascariensis (Choux) Choux, in A. C. White & B. Sloane, Stapelieae, ed. 1: 71. 1933. *Stapeliopsis madagascariensis* Choux, Compt. Rend. Hebd. Séances Acad. Sci. Paris 193: 1444. 1931. TYPE: Southern Madagascar. 15 km N of Ambovombe, Feb. 1931, *R. Decary s.n.* (holotype, P not seen). Figure 16.

Stems 25–100 mm long, 3–9 mm thick, procumbent often with ascending apices, grayish marked with purple-brown, surface bullate; tubercles broad and flattened, very indistinctly joined into 4 to 6 angles along stem, tapering abruptly into small, narrowly lanceolate, recurved leaf rudiment 1–2 mm long, which is slightly flattened above and gradually withers and falls off. *Pedicel* 3–6 mm long, 1.5 mm thick, spreading with erect apex holding flower facing upward; *sepals* 3–5 mm long, 1–2 mm broad at base, ovate-lanceolate, acute, smooth. *Corolla* 20–28 mm diam., shallowly campanulate; outside pale green to cream spotted with maroon (spots becoming finer toward base and apices of lobes); inside cream spotted with maroon (fading away in tube), covered except in tube with long, slender, white cylindrical papillae up to 2 mm

long with minute obtuse apical bristle; *tube* 4–7 mm long, 10–12 mm broad, bowl-shaped; *lobes* 6–9 mm long, 6–10 mm broad at base, broadly deltoid, acute, spreading to recurved; *corona* 3.5–4.0 mm tall, 4.5–6.0 mm broad, dark maroon, ± sessile; *outer lobes* ± 3 mm long, free practically to base, erect to slightly spreading, sometimes concave outside and slightly convex within, bifid at least to middle, with lobules narrowly deltoid and slightly diverging to obtuse and erect; *inner lobes* ± 0.6 mm long, narrowly deltoid to ± linear, sometimes exceeding anthers. *Seed* 3.0–5.0 × 2.5 mm, shortly pear-shaped, border slightly to very swollen, often paler than rest.

Distribution. Southern Madagascar, coastal region from Ambovombe to Itampolo but also southeast of Ihosy on southern edge of escarpment (Morat, 1995). Elevation 50–800 m.

Ecology. *Stapelianthus madagascariensis* may grow among small bushes in denuded areas. However, plants seem to grow equally well in accumulations of leaf litter on the floor of dry, xerophytic forest.

Discussion. The stems of *Stapelianthus madagascariensis* are generally prostrate with upturned apices and are indistinctly 4- to 6-angled. They form dense mats that may reach 300 mm in diameter.

Flowers of *Stapelianthus madagascariensis* are shallowly bowl-shaped, cream inside, and spotted all over with maroon. In some plants the spots fade in intensity in the tube, while in others they coalesce around the corona. Most of the inside (except toward the corona in the tube) is adorned with long, slender, often white, hair-like papillae. Outside, the corolla is also spotted brightly with red, but these spots do not correspond to those that are inside.

The outer corona lobes tend to be deeply bifid, usually for at least half their length.

Stapelianthus madagascariensis is most closely allied to *S. montagnacii*. The two species seem to be reliably separable by the indistinctly angled, often quite slender stems and the shallowly bowl-shaped flowers with small spots on a white background of *S. madagascariensis*. In *S. montagnacii* the stems are usually thicker and fairly clearly 4-angled, the flowers have a more deeply bowl-shaped tube, and they are darkly colored with pale mottling usually only near the base of the tube.

Specimens examined. MADAGASCAR. 0.5 km E of Saodona on road to Itampolo, 80 m, *Labat, du Puy & Phillipson 2096* (K); Tsihombe, *Bruyns 5958* (MO); 3–5 km from Behara, Sep. 1973, *Rakotozafy 1238* (TAN); Ampanihy, *Bosser 19227* (P).

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PHYLOGENY AND EVOLUTION OF *SYMBOLANTHUS* AND *WURDACKANTHUS* (GENTIANACEAE–HELIEAE) IN THE GUAYANA HIGHLANDS AND ANDES, BASED ON RIBOSOMAL 5S-NTS SEQUENCES[1]

Katherine R. Gould[2] and Lena Struwe[3]

Abstract

Symbolanthus (Gentianaceae, Helieae) is a genus of small trees, shrubs, and herbs distributed in South America (the central and northern Andes and the Guayana Highlands) and southern Central America. To discover the pattern of *Symbolanthus* evolution and to assess the relationships between *Symbolanthus* and the closely related *Wurdackanthus* of the Guayana Highlands (Venezuela, Brazil) and the Lesser Antilles (St. Vincent), we performed cladistic analyses on members of both taxa. Molecular data (5S-NTS rDNA sequences) were gathered from individual plant samples, mainly from herbarium specimens. 5S-NTS sequence data did not resolve internal relationships well in *Symbolanthus* and show that the genus may be a recently and rapidly diverging clade. However, these results indicate that *Wurdackanthus* is either paraphyletic to *Symbolanthus* or that *W. argyreus* is nested within a Symbolanthus clade. Furthermore, *W. frigidus* may be the basalmost species of the Wurdackanthus–Symbolanthus clade. This species is noticeably divergent and distinct, molecularly and morphologically, from the rest of the clade. Testing an alternate phylogenetic hypothesis in which *Wurdackanthus* is monophyletic results in trees 11 steps longer than the shortest trees found, and still with *Wurdackanthus* nested within *Symbolanthus*. Ancestral morphological character evolution in the Wurdackanthus–Symbolanthus clade is discussed in the context of a 5S-NTS consensus tree.

Key words: 5S-NTS, biogeography, Gentianaceae, Helieae, molecular systematics, morphology, Neotropics, phylogeny, *Symbolanthus*, *Wurdackanthus*.

Resumen

El género *Symbolanthus* (Gentianaceae, Helieae) incluye árboles pequeños, arbustos y hierbas, distribuidos en Sur América (al centro y norte de Andes y en las tierras altas de la Guayana) y al sur de Centro América. Con el objeto de descubrir el patron de la evolución y biogeografía de *Symbolanthus*, realizamos un análisis cladístico con algunas especies de *Symbolanthus* y del cercanamente relacionado *Wurdackanthus*, distribuido en las tierras altas de la Guayana (Venezuela, Brazil) y en las Antillas Menores (St. Vincent). Los datos moleculares (secuencias de 5S-NTS rADN) se obtuvieron de muestras individuales de plantas, principalmente de especímenes de herbario. Las secuencias de 5S-NTS no resolvieron bien las relaciones al interior de *Symbolanthus*, y mostraron que el género puede haber divergido rápida y recientemente. Estos resultados indican ya sea que *Wurdackanthus* es parafilético respecto a *Symbolanthus*, o que *W. argyreus* se encuentra dentro del clado de Symbolanthus. Mas aún, *W. frigidus* podria ser la especie más basal del clado Wurdackanthus–Symbolanthus. Esta especie es notoriamente diferente, tanto molecular como morfológicamente del resto del clado. Al probar una hipótesis alterna, en la cuál *Wurdackanthus* es monofilético, se encuentran árboles 11 pasos más largos que los mas cortos obtenidos, aún con *Wurdackanthus* incluído dentro de *Symbolanthus*. Con base en el consenso obtenido usando 5S-NTS, se discute la evolución de caracteres morfológicos ancestrales en el clado Wurdackanthus–Symbolanthus.

[1] We thank the herbaria of AAU, BM, F, HUH, K, MO, NY, S, U, US, USM, and WU for loans of plant material to LS, and NY and US for permission to remove leaf material from their sheets for DNA extraction. We are also grateful to Paul Berry for insightful comments on the manuscript, Jason R. Grant for unpublished information, and Rocio Cortez for Spanish translations. This work was funded by the National Science Foundation (award 0317612 to LS), Rutgers University, New Brunswick, New Jersey, and the Lewis B. and Dorothy Cullman Program for Molecular Systematics Studies, The New York Botanical Garden, New York.

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Symbolanthus G. Don (Gentianaceae) is a genus of about 30 species of small trees, shrubs, and (rarely) herbs distributed mainly in montane rain forests in the northern and central Andes (Bolivia, Colombia, Ecuador, Peru, Venezuela; ca. 21 spp.) and the Guayana Shield highlands in South America (Brazil, Guyana, Venezuela; 7 spp.), as well as southern Central America (Costa Rica, Panama; ca. 2–3 spp.). The Guayana Highland is one of the oldest land regions in South America, part of the original Gondwanan continent, which has not been inundated since the mid-Cretaceous (100 mya; Huber, 1995). The highland region comprises table mountains, known as tepuis, up to 3014 m altitude. Most tepuis consist of sandstones of the Roraima Formation overlying the Precambrian crystalline basement of the Guayana Shield (Ghosh, 1985). The age of the uplift of the sandstone plateau is unknown, but cycles of upheaval and erosion may go back to the Mesozoic (Kubitzki, 1989). Erosion of the sandstone resulted in the formation of isolated, vertical-cliffed mountains, the tepuis.

Symbolanthus is a member of the well-defined Helieae clade, which primarily consists of *Adenolisianthus* (Spruce ex Prog.) Gilg, *Aripuana* Struwe, Maas & V. A. Albert, *Calolisianthus* Gilg, *Chelonanthus* (Griseb.) Gilg, *Helia* Mart., *Irlbachia* Mart., *Macrocarpaea* (Griseb.) Gilg, *Rogersonanthus* Maguire & B. M. Boom, *Symbolanthus*, *Tachia* Aubl., *Tetrapollinia* Maguire & B. M. Boom, and *Wurdackanthus* Maguire (Struwe et al., 1997, 2002). Helieae are exclusively Neotropical with the highest concentration of genera on the Guayana Shield. They include the majority of non-montane Neotropical gentians and contain among the highest morphological and anatomical diversity within the family. Many Helieae, as well as *Symbolanthus*, species are endemic to single mountain tops, ridges or massifs, river drainages, or islands. *Symbolanthus* infrageneric taxonomy is fraught with difficult species delimitation problems, particularly among Andean entities, and many undescribed species (Struwe, 2003a, b).

Symbolanthus and the morphologically similar *Wurdackanthus* together form a well-supported clade within Helieae (Struwe et al., 2002; Fig. 1). They can be distinguished from other Helieae and gentians by pollen morphology and the presence of a corona or corona-like structure within the corolla. *Wurdackanthus* differs from *Symbolanthus* in having a much shorter calyx that is divided ¾ of its length, as opposed to being divided ⅞ or more of its length (Pringle, 1995; Struwe et al., 1999). *Wurdackanthus* consists of two species, *W. argyreus*, which is endemic to the Guayana Highlands, and *W. frigidus*, found in the Lesser Antilles.

Our objectives in this study are to determine the phylogenetic relationship between *Symbolanthus* and *Wurdackanthus*, which share morphological characteristics that are unique within Helieae, and to investigate these putative synapomorphies in a phylogenetic context with a known outgroup, *Chelonanthus* (Struwe et al., 2002). Previous cladistic analyses of Helieae with nrDNA sequences of the internal transcribed spacer (ITS) region showed that this gene region, though highly variable in other Helieae lineages, including *Macrocarpaea* (Grant & Struwe, 2000), does not vary enough within *Symbolanthus* to resolve interspecific relationships (Struwe et al., 2002; Fig. 1). In order to assess relationships within *Symbolanthus*, it was necessary to use a more quickly evolving DNA fragment. DNA of the ribosomal 5S non-transcribed spacer (5S-NTS) region has been shown to be highly variable in closely related species of plants (e.g., *Alibertia* A. Rich., Persson, 2000; *Saintpaulia* Wendl., Lindqvist & Albert, 1999; see also Cox et al., 1992; Kellogg & Appels, 1995; Cronn et al., 1996). Like ITS sequences, 5S-NTS sequences are arranged in arrays of several hundred to several thousand tandemly repeated copies that occur at one or several chromosome loci and that normally become homogenized via concerted evolution processes (Hillis & Dixon, 1991; Playford et al., 1992).

Materials and Methods

Molecular Methods

Due to the remote habitats of many *Symbolanthus* and *Wurdackanthus* species, we relied on DNA extraction from leaf material from herbarium sheets (Table 1). Total DNA was extracted from 0.5–1 cm^2 dried leaf tissue. Leaves were pulverized by means of a Bio 101/Savant FastPrep tissue disruptor, followed by extraction with a CTAB (cetyldimethylammonium bromide) buffer with the addition of 1% PEG 4000 (polyethylene glycol), and glassmilk (GeneClean, Bio 101) purification (modified from Struwe et al., 1998). For difficult samples, a chloroform:isoamyl alcohol (24:1) purification step was added following CTAB extraction. Amplification of the 5S-NTS region by polymerase chain reaction (PCR) was accomplished in standard 25 µl reactions on a Perkin Elmer Gene Amp 9600 in the presence of bovine serum albumin (BSA, 0.04%) and tetramethyl ammonium chloride (TMACl, 0.1 mM). PCR primers were "5S forward" and "5S reverse" designed by Cox et al. (1992). The cycle program included an initial incubation at 95°C for

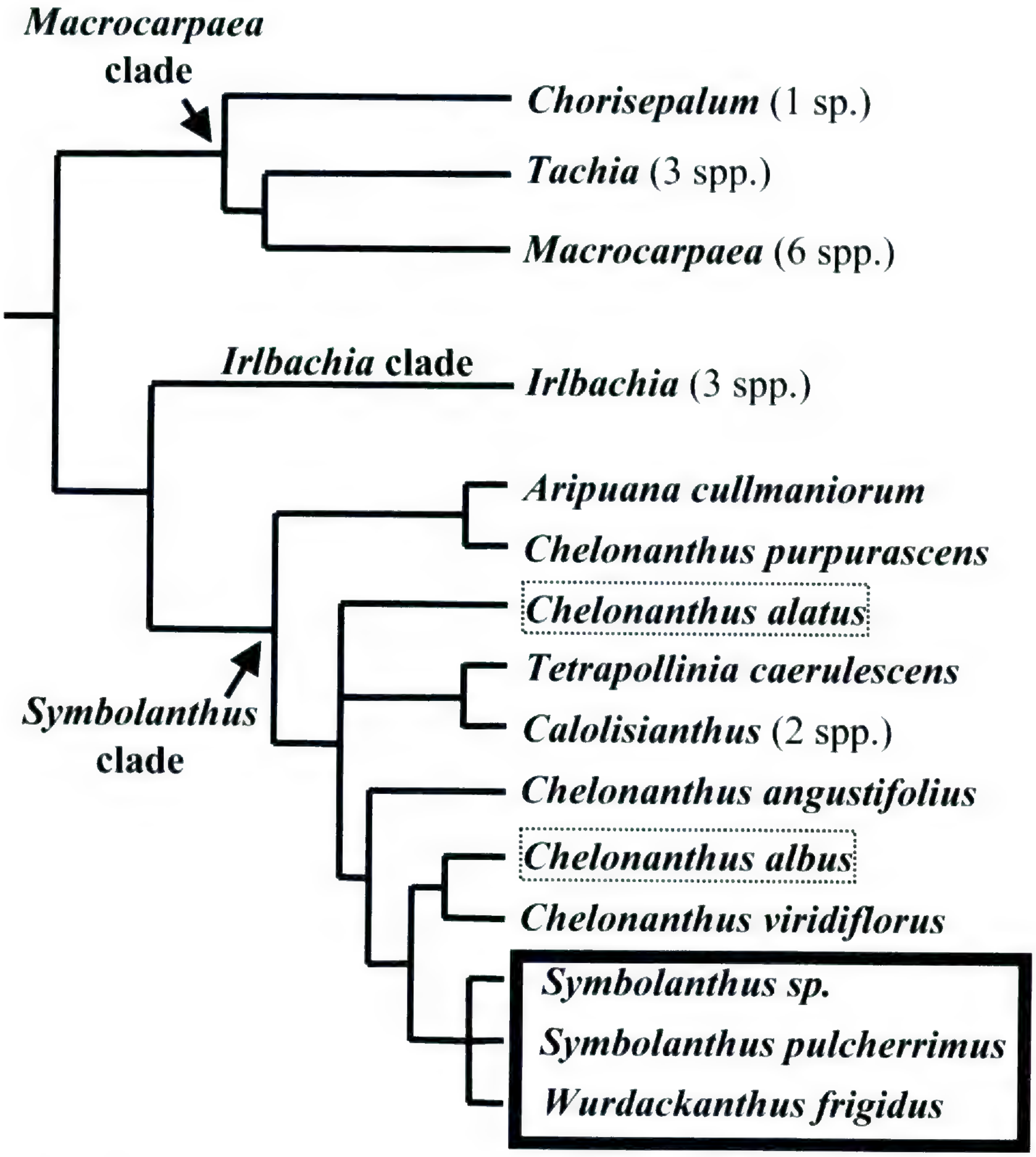

Figure 1. Preliminary phylogenetic relationships of the Helieae based on ITS sequences (adapted after Struwe et al. (2002) and L. Struwe, K. Gould, J. R. Grant & V. A. Albert, unpublished). Within Helieae, three major well-supported clades are identified, the Macrocarpaea clade, the Irlbachia clade, and the Symbolanthus clade (Struwe et al., 2002). The genus *Chelonanthus* is paraphyletic within the Symbolanthus clade; the two species used in this study are indicated with dotted boxes. The Symbolanthus–Wurdackanthus clade is indicated with a solid box.

2 min., followed by 27 cycles of 94°C for 1 min., 60°C for 1 min., and 72°C for 1 min.

Most PCR products were run on a low-melting agarose (1.2%) gel, from which the fragments were plugged, resuspended in 300 µl water, and reamplified as before to increase product yield. PCR products were then prepared for sequencing by column purification using QIAquick spin-columns (Qiagen). This was followed by PCR-based cycle sequencing reactions using a d-Rhodamine Terminator Cycle Sequencing Ready Reaction kit (Perkin Elmer Applied Biosystems) with AmpliTaq DNA polymerase, FS, following kit protocols, and using the same PCR primers. Sequencing reactions were cleaned by means of Sephadex (Pharmacia Biotech AB) column purification.

Sequencing gels were run on an ABI 377 XL automated sequencer. Sequences obtained were edited and aligned using the software program Sequencher 3.0 (GeneCodes Corp.). Only clearly readable sequences were used. The aligned sequences were cut at an arbitrarily chosen position at both ends of the spacer where all sequences were readable. The complete alignment is available at <http://www.rci.rutgers.edu/~struwe/dnadata.htm>. All molecular-based phylogenetic work was done at the Lewis B.

and Dorothy Cullman Program for Molecular Systematics Studies of the New York Botanical Garden. Table 1 lists the species, voucher specimens, and Genbank accession numbers of sequences used in the study.

Eleven individuals and nine species of *Symbolanthus* and both species of *Wurdackanthus* were sampled. Attempts to amplify 5S-NTS for additional species of *Symbolanthus* from herbarium material (in particular from tepui species) failed, presumably due to poor specimen preservation. Two species of *Chelonanthus* were used as outgroups following sister-group relationships derived from ITS data (Struwe et al., 2002; Fig. 1). Thus a total of 15 individuals representing 13 species were included in the 5S-NTS data set. Species of *Calolisianthus* and *Tetrapollina caerulescens* (Aubl.) Maguire & B. M. Boom were also sequenced for 5S-NTS, but were very divergent from and therefore difficult to align with *Symbolanthus* and *Chelonanthus* and were not included in the analysis. During the course of this study, four undescribed species of *Symbolanthus* were identified among our herbarium samples. They are here indicated as "sp. ined. 1–4" (Table 1) and will be described in a later publication on the taxonomy of *Symbolanthus*.

Phylogenetic analyses were done using maximum parsimony in PAUP* version 4.0b4a (Swofford, 2000). Minimal length trees were searched for using the heuristic option, with TBR branch-swapping, 100 replicates of random addition sequence order, and branches collapsed if the maximum branch length is zero. Gaps in the aligned 5S-NTS sequences were treated as missing data. Branch lengths were calculated using the ACCTRAN option in PAUP*.

Internal clade support was evaluated using the parsimony jackknifing procedure, which was performed in Xac (Farris et al., 1996), using 1000 replicates with 5 random addition replicates each. Decay analyses (Donoghue et al., 1992) were done in PAUP* by means of the AutoDecay program (Eriksson, 1998). In addition, analyses were run with topological constraints imposed, first forcing *Wurdackanthus* and then *Symbolanthus* to be monophyletic, to determine their effects on tree lengths and to test alternate hypotheses of relationships. Heuristic searches were done with these constraints imposed and all other run options as above.

MORPHOLOGICAL METHODS

Morphological data were collected by examining the same specimens that were sequenced, as well as duplicates of the same collections and pickled flower and fruit material from the same collection when available. Output trees from PAUP* were imported into MacClade version 3.08a (Maddison & Maddison, 2000) in order to explore changes among morphological character states. Thirty vegetative and reproductive characters were examined, including five quantitative characters. Measurements for quantitative characters were divided into discrete ranges by means of two different methods described in Chappill (1989) (gap-coding and segment-coding) and coded as discrete character states.

RESULTS

5S-NTS

The aligned data set of the 5S-NTS region contains 322 characters, including 139 (43%) variable characters and 55 (17%) parsimony-informative characters. However, most of the variation found represents differences between the outgroup, *Chelonanthus*, and *Wurdackanthus–Symbolanthus*, as well as between *W. frigidus* and the remaining ingroup taxa (see below). Individual sequence lengths for the 5S-NTS region range from 292 bp (*Chelonanthus alatus*) to 311 bp (*Symbolanthus nerioides*), with most taxa having a length of 308 bp. Mean GC content for the data set calculated in PAUP* is 57%.

PARSIMONY ANALYSES

Results of the parsimony analyses are shown in Figure 2. The parsimony analysis of the 5S-NTS data set alone yielded 42 shortest trees of length 186 (consistency index excluding uninformative characters (CI) = 0.86, retention index (RI) = 0.85; Fig. 2A, B). In the strict consensus tree (Fig. 2A), with *Chelonanthus* spp. as outgroup, *Wurdackanthus frigidus* (St. Vincent) is sister to the remaining taxa, with 100% jackknife support and a decay value of 30. *Wurdackanthus argyreus* (Guayana Highlands: Sierra de la Neblina and Cerro Aracamuni) and all *Symbolanthus* species form a clade (jackknife = 100%, decay = 8) within which there is little resolution. However, two clades with good measures of support are found, one containing the two *S. macranthus* samples (Ecuadorean cloud forest species; jackknife = 73%), and a second containing two Central American species, *S. pulcherrimus* (Cartago region of Costa Rica) and *S.* sp. ined. 1 (Veraguas, Panama) (jackknife = 98%, decay = 4). Overall, there is relatively little molecular divergence within the W. argyreus + Symbolanthus clade, with the exception of a long terminal branch

Table 1. Material used in this study.

Taxon	Country, State	Locality	Collector #	Herbarium voucher at:	GenBank number
Chelonanthus alatus (Aubl.) Pulle	French Guiana	Saül (3°37′N, 53°12′W) and vicinity, on road to airport	*S. A. Mori et al. 24076*	NY	AY143381
Chelonanthus albus (Spruce ex Prog.) Badillo	Brazil, Amazonas	Rio Negro between Manaus and São Gabriel, ca. 80 km N of São Gabriel, ca. 100 m alt., terra firme, 00°20′N, 66°45′W	*J. M. Poole 2049*	NY	AY143384
Wurdackanthus argyreus Maguire	Venezuela, Amazonas	Cerro de la Neblina, 6.5 km SSE of base camp, southern extension of range, elev. 1600 m, 0°47′N, 66°11′W, ridge top with bromeliads, *Heliamphora* and low shrubs	*B. Stein et al. 1617*	NY	AY143371
Wurdackanthus frigidus (Sw.) Maguire & B. M. Boom	St. Vincent	Charlotte Parish, on the W slope of Soufriere Mountain among scrub vegetation	*G. R. Cooley 8211*	NY, S	AY143370
Symbolanthus sp. ined. 1	Panama, Veraguas	Along road between Escuela Agricola and Alto Piedra (above Santa Fe) and Río Dos Bocas ca. 5–8 km from Escuela, 730–770 m elev.	*T. B. Croat 25922*	AAU, MO, NY	AY143382
Symbolanthus sp. ined. 2	Peru, Pasco	Border Prov. Oxampampa and Pasco, in dwarf forest, elev. 2700 m. Rich in Ericaceae, bamboo and *Blechnum*, with *Sphagnum* layer below, San Cotardo	*H. van der Werff et al. 8511*	F, MO, US	AY143378
Symbolanthus sp. ined. 3	Peru, Loreto	Província Requena, Distrito Sapuena, Poblado Jenaro Herrera, CIJH-IIAP, bosque de altura area W of herbarium, elev. ca. 200 m	*P. Aevedo & D. Daly 1592*	NY	AY143372
Symbolanthus sp. ined. 4	Bolivia, La Paz	Prov. Sud Yungas, 9 km from Huancané (16°22′S, 67°32′W) on the road to San Isidro, 2540 m, "Bosque de alta montaña con Podocarpus"	*L. J. Dorr et al. 6691*	NY	AY143383
Symbolanthus macranthus 1 (Benth.) Moldenke	Ecuador, Loja	Road to Cerro Toledo, 8–11 km from turnoff above town of Yangana, ca. 4°20′S, 79°10′W, 2440–2700 m, scrub vegetation and cloud forest	*J. L. Luteyn et al. 15099*	NY	AY143373
Symbolanthus macranthus 2 (Benth.) Moldenke	Ecuador, Zamora–Chinchipe	Road between Loja & Zamora ca. km 16–18, ecotone beween cloud forest and páramo, elev. 2500–2650 m	*J. L. Luteyn et al. 6620*	NY	AY143375
Symbolanthus brittonianus Gilg	Bolivia, La Paz	Prov. Larecaja, 19.0 km al SO de Guanay por el camino a Tipuani, bosque húmedo, 15°34′S, 67°59′W, 1200 m	*J. C. Solomon 17684*	MO, NY	AY143376
Symbolanthus pulcherrimus Gilg	Costa Rica, Cartago	Cantón del Guarco, Distrito de San Isidro, bosque secundario y robledales alterados en las cercanías de El Empalme, 9°43′04″N, 84°03′01″W, 2300 m	*J. F. Morales et al. 1600*	F, MO, NY (×2)	AY143379
Symbolanthus nerioides 1 (Griseb.) Ewan	Venezuela, Mérida	Cloud forest in sheltered valley, Estanques–Paramis de los Colorados Road, alt. ca. 2300 m	*G. L. Sobel & J. Strudwick 2164*	NY	AY143377
Symbolanthus nerioides 2 (Griseb.) Ewan	Venezuela, Mérida	Distrito Sucre, along carretera Estanque a El Molino, just E of Páramo Molino, elev. ca. 2500 m	*G. R. Proctor et al. 49150*	US	AY143380
Symbolanthus vasculosus Gilg	Venezuela, Barinas	Distrito Bolívar, Municipio Altamira, "La Gallineta," Caserio "El Celosos" near feldspar mine, ca. 1700 m elev. [ca. 8°50′N, 70°35′W]	*L. J. Dorr et al. 5474*	NY, US	AY143374

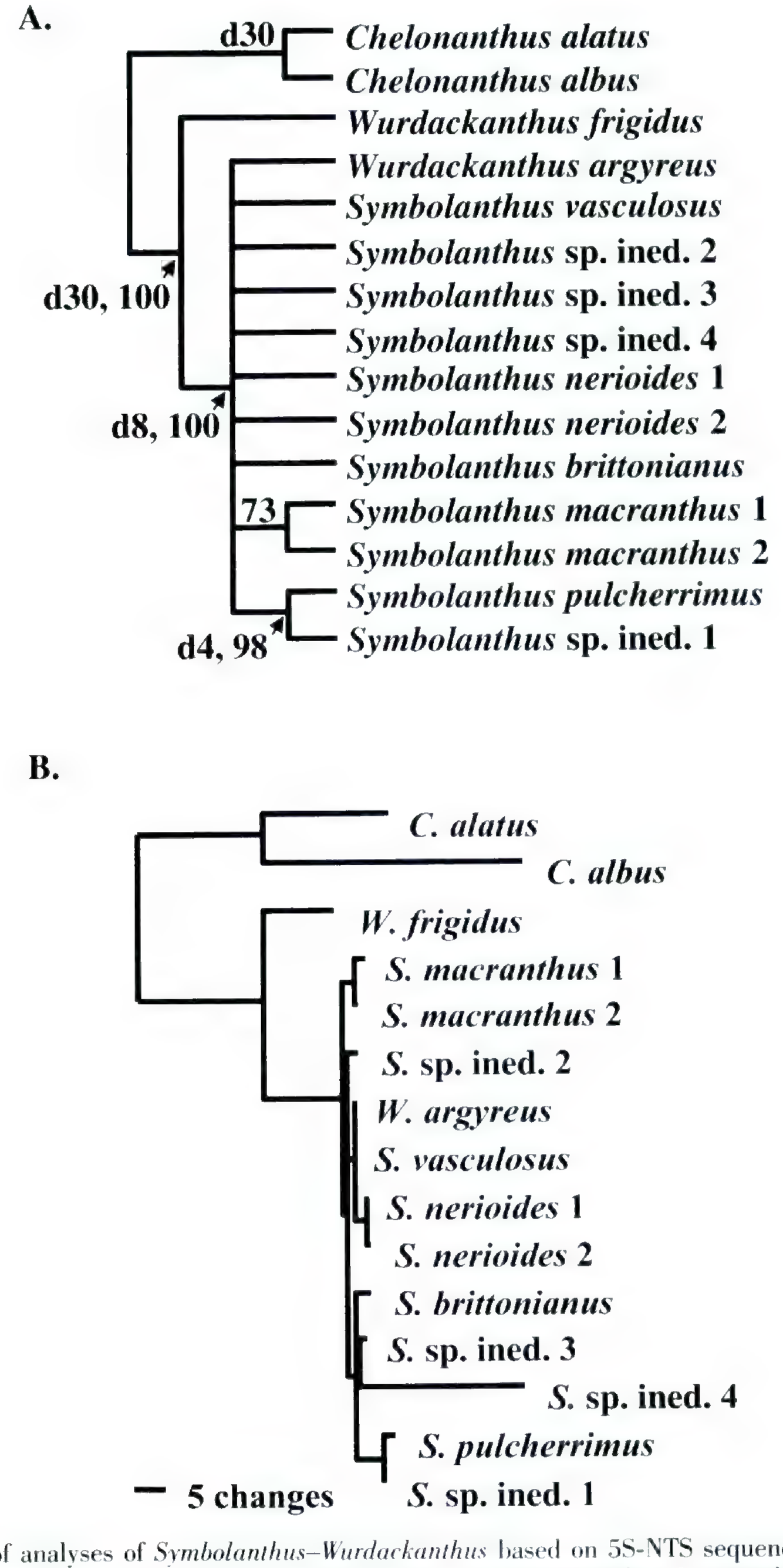

Figure 2. Results of analyses of *Symbolanthus–Wurdackanthus* based on 5S-NTS sequence data. —A. Strict consensus tree showing support indices for nodes including decay values greater than 1 (preceded by "d") and jackknife values greater than or equaling 50%. —B. Tree showing branch lengths for one of 42 shortest trees from the 5S-NTS analysis.

leading to *Symbolanthus* sp. ined. 4 (Bolivian Andes), containing 28 changes (Fig. 2B). Notably, there is a relatively large amount of divergence between the two species of *Wurdackanthus*, with a long branch containing 13 changes between *W. frigidus* and *W. argyreus* + *Symbolanthus*.

CONSTRAINT ANALYSES

The first constraint analysis kept only trees compatible with a pre-defined *Wurdackanthus* monophyly constraint tree. PAUP* found 491 trees of length 197, 11 steps longer than the most parsimonious trees (CI = 0.76, RI = 0.71). In all of

these trees, a Wurdackanthus clade is nested within a Symbolanthus clade, making *Symbolanthus* paraphyletic.

The second constraint analysis kept only trees compatible with a pre-defined *Symbolanthus* monophyly constraint tree. PAUP* found 30 trees of length 187, one step longer than the most parsimonious trees (CI = 0.85, RI = 0.84). In all of these trees, *Wurdackanthus* is paraphyletic toward *Symbolanthus*, with *W. frigidus* most basal followed by *W. argyreus*.

In summary, results indicate that *Wurdackanthus* is paraphyletic, with *W. frigidus* sister to a W. argyreus + Symbolanthus clade. *Wurdackanthus argyreus* is either sister to the *Symbolanthus* species or nested among them. The constraint analysis forcing *Wurdackanthus* to be monophyletic finds trees much longer than the most parsimonious trees and results in a non-monophyletic *Symbolanthus*.

MORPHOLOGICAL ANALYSES

Eight characters out of 30 that were examined were found to be potential synapomorphies for clades. These characters were corolla length, calyx length, depth of calyx division, number of flowers per inflorescence, capsule length, pollen type, presence of corona or staminal pockets inside the corolla, and flower bud shape (see Fig. 3). The different means of coding quantitative character states did not affect the outcome of the analysis of synapomorphies.

Discussion

PHYLOGENY

Sequencing of the 5S-NTS region has now been done within three genera of Helieae, including the two largest, *Symbolanthus* and *Macrocarpaea*. We expected 5S-NTS data to be useful for resolving both higher- and lower-level relationships. For example, the 5S-NTS data do indicate the paraphyly of *Wurdackanthus* toward *Symbolanthus*. Because a monophyletic *Wurdackanthus* is not supported by these data, and because of its morphological and anatomical similarities to *Symbolanthus*, its circumscription should be reconsidered (Struwe & Gould, 2004).

However, we found that in Helieae, 5S-NTS data also highlighted the accumulation of different amounts of molecular change in lineages of presumably different ages. While there is little variation within *Symbolanthus*, considerably more variation occurs within *Macrocarpaea* (J. R. Grant & L. Struwe, unpublished), which based on relative amounts of ITS variation (Grant & Struwe, 2000) is estimated to be a relatively much older lineage.

We did find a relatively large amount of molecular change between *Chelonanthus* and *Wurdackanthus–Symbolanthus* (branch length = 39), as well as between the two species of *Chelonanthus* we sampled (branch length = 27; see Fig. 2B), indicating that the 5S-NTS region can be useful in phylogenetic studies at higher levels, e.g., between closely related genera. Many changes also occurred along the branch between *Wurdackanthus frigidus* and *W. argyreus* + *Symbolanthus* (13), signifying a greater divergence between the two species of *Wurdackanthus* than between *W. argyreus* and *Symbolanthus* spp.

MORPHOLOGY

Compared to the outgroup, *Chelonanthus*, potential synapomorphies for the Wurdackanthus–Symbolanthus clade include having long corollas (greater than ca. 3 cm) and relatively large capsules. Other synapomorphies that distinguish *Wurdackanthus–Symbolanthus* from all other Helieae are common presence of a corona or staminal pockets inside the corolla and pollen of *Symbolanthus*-type (i.e., pollen grains united in tetrahedral tetrads with strongly reticulate exine; Nilsson, 1970) (Fig. 3).

Potential synapomorphies for the Wurdackanthus argyreus + Symbolanthus clade include even longer corollas (5.7 cm long or greater), pointed flower bud apices, and 1 to 3 flowers per inflorescence (vs. 5 or more) (Fig. 3). *Chelonanthus* bears many flowers per inflorescence on 1 to 4 long monochasial branches within a dichasium, and *Wurdackanthus frigidus* produces up to 7 flowers on monochasial branches, while *Wurdackanthus–Symbolanthus* have reduced 1- to 3-flowered mono- or dichasia. Deeply divided calyces is another possible synapomorphy for the W. argyreus + Symbolanthus clade (calyces divided 2/3 to nearly all the way to the base vs. 1/3 divided in *W. frigidus*; Fig. 3), but *Chelonanthus* is polymorphic for this character.

These morphological changes, as well as the relatively large number of nucleotide base changes along the branch to this clade, indicate that *Wurdackanthus argyreus* and *W. frigidus* are relatively divergent from one another. The character of calyx length has been used in the literature to separate *Wurdackanthus* from *Symbolanthus*, *Symbolanthus* having a longer calyx (e.g., Pringle, 1995; Struwe et al., 1999). However, according to our results, the relatively short calyx of *Wurdackanthus* is a plesio-

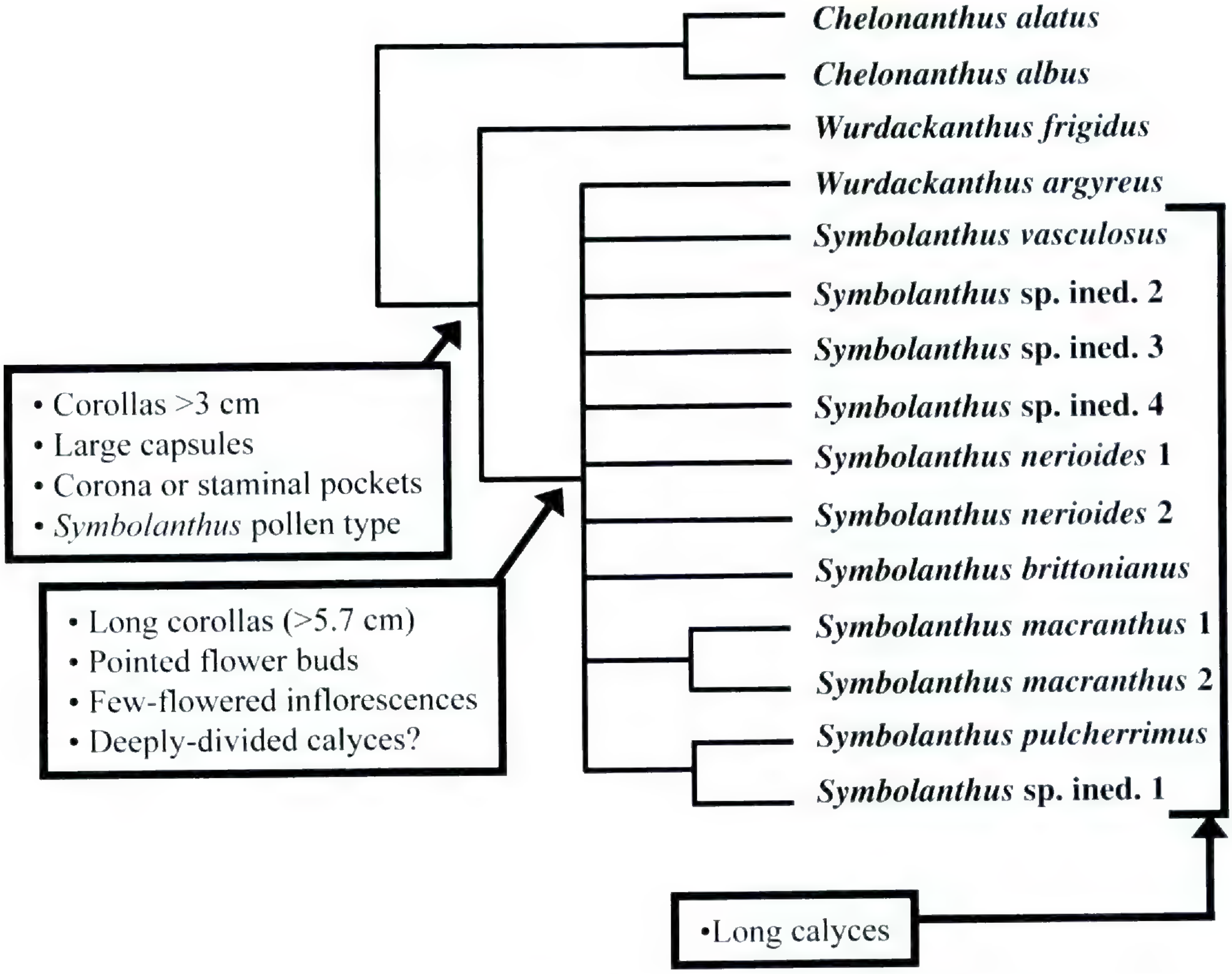

Figure 3. Potential morphological synapomorphies for *Wurdackanthus* + *Symbolanthus*, *W. argyreus* + *Symbolanthus* and *Symbolanthus* based on the 5S-NTS strict consensus tree.

morphic character state that is also found in *Chelonanthus*, not a synapomorphy for *Wurdackanthus* (Fig. 3). Although the two species of *Wurdackanthus* are relatively divergent from one another morphologically and in 5S-NTS sequences, other molecular data sets support a close relationship between *W. frigidus* and *Symbolanthus* spp. (nrITS sequences and cpDNA *trn*L intron sequences, Struwe et al., 2002).

BIOGEOGRAPHY

The *Symbolanthus* distribution is an excellent opportunity to test the influence of migration between the Guayana Highlands, the Andes, and Central America, and to test biogeographic hypotheses about the origin of the Guayana Highland flora. This study indicates the possibility that tepui species could have had Andean origins, since *Wurdackanthus argyreus* (Sierra de la Neblina and Cerro Aracamuni) is not consistently basal but nested among non-tepui *Symbolanthus* species. In the 50% majority rule consensus tree, it is nested among two Venezuelan Andean species (*S. nerioides* and *S. vasculosus*). Future research directions on this group would be to obtain better material of tepui species for DNA sampling, or use morphological data to make a phylogeny of all species once a revision of *Symbolanthus* is complete (Struwe, in prep.). In addition, a higher-resolution data set, such as AFLPs, would probably be helpful.

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VIII INTERNATIONAL AROID CONFERENCE, MISSOURI BOTANICAL GARDEN, ST. LOUIS, 9–11 AUGUST 1999: INTRODUCTION

Thomas B. Croat[1]

The VIII International Aroid Conference, organized by Tom Croat of the Missouri Botanical Garden, was held in August 1999, the week following the XVI International Botanical Conference in St. Louis. Over 125 attendees from 21 countries participated in three days of paper sessions, poster presentations, greenhouse tours, and social events.

Oral presentations were made in six general areas: 1. Araceae of general areas, including aroids in South America, the Mediterranean Region, North America, the Indian Subcontinent, Africa, and Madagascar. 2. Aroid collections, horticultural and herbarium, including South Florida, Marie Selby Botanical Gardens, the Royal Botanical Garden, Kew, the botanical gardens in Munich and Brussels, Russia, and Australia. A special presentation was made by Tony Avent of Juniper Level Botanical Garden. 3. Morphology, systematics, and evolution, including papers on *Rhodospatha*, *Raphidophora*, *Philodendron* subg. *Pteromischum*, *Amorphophallus*, *Arisaema*, *Dracontium*, shoot morphology in Brazilian root-climbing Araceae, comparative vegetative anatomy, and molecular systematics of the *Caladium* alliance. 4. Araceae of specific areas, including papers on the Araceae of the Flora of China, Brunei, central Brazil, Ecuador, Thailand, Western Ghats, India, Bajo Calima in Colombia, Vietnam, and Chiapas State in Mexico. 5. Aroid breeding and horticulture, including research with potted ornamental plant breeding, the *Anthurium* cut-flower industry in Holland, taro production in Hawaii, micropropagation of Araceae, biotech breeding of *Anthurium*, and cultivation of *Arisaema*. 6. Miscellaneous, including papers on pollination ecology of the Araceae, insects associated with Araceae, registration of hybrid plants, investigations in *Arum*, studies with tribe Lasioideae, *Amorphophallus* in China, acids of seed lipids in Araceae, comparison of two models for chromosomal evolution in Araceae, revision of *Homalomena*, taxonomy and phylogeny of *Philodendron* sect. *Calostigma* in Brazil, Aroid-L and the International IAS Society webpage, and finally, a roundtable discussion of the IAS webpage development.

A total of 45 posters were presented on a wide variety of subjects dealing with Araceae and were displayed during all three days of the conference.

The scientific papers presented in this issue were among the presentations at the conference; the remaining papers will be published in *Aroideana*. The offerings included here are Felipe Cardona's "Synopsis of the genus *Spathiphyllum* (Araceae) in Colombia"; Eduardo G. Gonçalves's "Araceae from central Brazil: Comments on their diversity and biogeography"; R. J. Henny et al.'s "Progress in ornamental plant breeding research"; and three papers addressing anatomical research of Araceae, namely, Eduardo G. Gonçalves et al.'s "A preliminary survey of petiolar collenchyma in the Araceae," and Richard C. Keating's "Vegetative anatomical data and its relationship to a revised classification of the genera of Araceae" and "Systematic occurrence of raphide crystals in Araceae."

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SYNOPSIS OF THE GENUS *SPATHIPHYLLUM* (ARACEAE) IN COLOMBIA[1]

Felipe Cardona[2]

Abstract

The last revision of *Spathiphyllum* was published over 40 years ago, and there is considerable need for additional new work throughout the tropics. Preliminary results are here presented toward the genus *Spathiphyllum* in Colombia, where 18 of the 50 known species occur. In this geographical region, all species appear restricted to the lowland to middle-elevation forests of interandean valleys, Amazonia and Chocó regions, from sea level to 1300 m. The middle Río Magdalena valley in northwestern Colombia, with 9 species, exhibits the highest concentration of taxa. Species of *Spathiphyllum* grow in partially or periodically flooded primary forests and in sites with low light intensities. Four sections of the genus *Spathiphyllum* occur in Colombia: sect. *Amomophyllum*, sect. *Massowia*, sect. *Dysspathiphyllum*, and sect. *Spathiphyllum*. Five species are from elsewhere in the Amazonian region of South America, and 11 other species appear widely distributed in Central America.

Key words: Araceae, Colombia, *Spathiphyllum*.

Resumen

La última revisión de *Spathiphyllum* fue publicada hace 40 años y hay una considerable necesidad de nuevos trabajos para el trópico. Se presentan los resultados preliminares para el género *Spathiphyllum* en Colombia, donde el género está representado por 18 de las 50 especies conocidas. En esta región geográfica todas las especies están restringidas a los bosques de tierras bajas de los valles interandinos, la Amazonia y la región del Chocó, desde el nivel del mar hasta 1300 m. El valle medio del Río Magdalena en el NO del país, con 9 especies, presenta la más alta concentración. Las especies de *Spathiphyllum* crecen en sitios parcial o periódicamente inundados con bajas intensidades de luz. Cuatro secciones del género se encuentran en Colombia: sect. *Amomophyllum*, sect. *Massowia*, sect. *Dysspathiphyllum* y sect. *Spathiphyllum*. Cinco especies se conocen para la Amazonia y 11 aparecen ampliamente distribuidas en América Central.

Colombia has the richest assemblage of Araceae species (Croat, 1992) of any Neotropical country. At least two genera, *Anthurium* Schott and *Philodendron* Schott, exhibit their highest concentration of taxa here. Despite the wealth of information regarding Araceae in Colombia, few genera have been thoroughly studied. Here I present preliminary data on the genus *Spathiphyllum* Schott in Colombia. *Spathiphyllum* is widely distributed in Colombia, occurring from sea level to 1300 m, but is most common in lowland forests, where it is closely associated with streams, often forming large colonies. The taxonomy of the group is rather difficult, and the gross morphological characters used in the most recent revision of the genus (Bunting, 1960) require further examination. The present author is working to complete a taxonomic revision of the genus for the *Flora of Colombia*, the preliminary results of which are presented below.

Spathiphyllum includes 50 species that exhibit a tropical distribution; 47 species are restricted to the Neotropics and the three remaining to the Philippines and Indonesia (pers. obs.). *Spathiphyllum* is easily distinguished from other genera in the family by the combination of bisexual flowers (with perianth), a persistent foliaceous spathe, the sheathing portion of the petiole, which is ⅔ or more the total petiole length, inaperturate striate pollen, and terrestrial habit. Grayum (1990), Bogner and Nicolson (1991), and Mayo et al. (1997) all seem to agree that the genus appears most closely related to the Indomalesian *Holochlamys* Engl.

[1] I am grateful to Thomas B. Croat (MO) and Ricardo Callejas (HUA), who carefully read the manuscript and provided valuable suggestions. Data were gathered from fieldwork by the author in the Andean region of Colombia, complemented with relevant literature and collections from all major herbaria in the country (COAH, COL, HUA, JAUM, MEDEL), as well as the TROPICOS database. A visit to MO was possible thanks to an Alwyn Gentry fellowship, and financial support for fieldwork in Antioquia and Chocó was provided by the Comité de Investigaciones at the Universidad de Antioquia.

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Nine species of *Spathiphyllum* have been described from the Neotropics since Bunting's (1960) revision of the genus, which treated 36 taxa; however, our knowledge of the ecology, reproductive biology (Montalvo & Ackerman, 1986), evolutionary trends, and taxonomy of the group remains almost unchanged.

Spathiphyllum is known in Colombia by 18 species. Despite intensive collecting in the area during the last three decades, some taxa remain known only from the type collections. Most species of *Spathiphyllum* are cultivated, not only because they are easily propagated, but also because of their attractive, dark green, glossy foliage, in strong contrast with the pure white to greenish spathes and spadix. Not surprisingly, many Colombian species of *Spathiphyllum* were described from material collected by European botanists in the 19th century searching for ornamental plants that could be introduced to that continent. Unfortunately, due to the vagueness of the horticultural trade in the past century, data on specific localities is often poor or simply absent. Briefly I here provide data on geographical distribution and the state of knowledge for all species of the genus known from Colombia.

Spathiphyllum Schott, Melet. Bot. 22. 1832. TYPE: *Spathiphyllum lancaefolium* (Jacq.) Schott.

Terrestrial herb; rhizome creeping, often just below the surface of the ground, the plant appearing to be acaulescent; internodes short; roots emerging through the petiole bases; leaves several, mostly erect to erect-spreading; petioles often fully sheathed, with apical geniculum; blades oblong to elliptic to narrowly elliptic, acuminate at apex; midrib sunken above, narrowly raised below; primary lateral veins moderately numerous, extending to the margins; interprimary veins and minor veins nearly always present; higher-order veins transverse-reticulate. Inflorescence solitary; peduncles as long as or longer than leaves; spathe oblong-elliptic to elliptic or obovate, acuminate at apex, acute to obtuse or rounded and sometimes conspicuously decurrent at base, midrib and primary lateral veins white or green but turning green in fruit; spadix cylindrical, erect, shorter than spathe, stipitate, rarely sessile, stipe often adnate in part to the spathe; flowers bisexual, perigonate; tepals 4 to 6, arching over pistil and rarely fused into a ring; stamens 4 to 6, free, filaments short, flattened; connective slender; thecae oblong-ellipsoid to ovoid, dehiscing by longitudinal slit; pollen inaperturate, ellipsoid to ellipsoid-oblong; gynoecium ovoid, subcylindrical, obovoid or flask-shaped; ovary 3-locular, rarely 2- to 4-locular, ovules 2, 4, 6, or 8 per locule, anatropous to hemianatropous; placentation axile; style conical and sometimes prominently exserted, sometimes truncate; stigma 2- or 3-lobed or subcapitate. Berries 1- to 8-seeded, greenish; seeds oblong, elliptic to ovate or reniform, pale yellow to brown, striate-verrucose; embryo axile, elongate, slightly curved; endosperm copious.

KEY TO THE SECTIONS OF *SPATHIPHYLLUM* IN COLOMBIA

1a. Perianth segments totally connate ..... I. sect. *Massowia*
1b. Perianth segments free, at least at the apex.
  2a. Pistil truncate to subtruncate or blunt and scarcely exceeding the perianth.
    3a. Apex of the pistil truncate to sub truncate ..... II. sect. *Amomophyllum*
    3b. Apex of the pistil blunt ..... III. sect. *Dysspathiphyllum* (*S. humboldtii*)
  2b. Pistil attenuate or conical and exceeding the perianth ..... IV. sect. *Spathiphyllum*

I. Spathiphyllum sect. **Massowia** (K. Koch) Engl., in DC., Monogr. Phan. 3: 228. 1879. TYPE: *Spathiphyllum cannaefolium* (Dryand) Schott.

KEY TO THE SPECIES OF *SPATHIPHYLLUM* SECT. *MASSOWIA* IN COLOMBIA

1a. Primary lateral veins arising at 25–45°; Amazonia ..... 1. *S. cannifolium*
1b. Primary lateral veins arising at 50–65°; Antioquia and Chocó ..... 2. *S. laeve*

1. Spathiphyllum cannifolium (Dryand.) Schott, Gen. Aroid. 1: 1. 1853 [as "*cannaefolium*"]. *Pothos cannifolius* Dryand., Bot. Mag. 17, t. 603. 1803. TYPE: "Hort. Kew, 1790" (holotype, BM not seen).

Likely the most widespread species of the genus in Colombia, *Spathiphyllum cannifolium* appears restricted to the Amazon basin, where it is known from practically all major tributaries of the Amazonas, Caquetá, Vichada, Apaporis, and Guayabero Rivers. A large gap in distribution exists, however, in the central portion of the Colombian Orinoco and Caquetá valleys, likely due to poor collecting in the area.

In Colombia, *Spathiphyllum cannifolium* occurs at 200 to 1000 m elevation, in tropical wet forest life zones, and flowers all year round.

Representative specimens examined. COLOMBIA. **Amazonas:** Río Igara-Parana, afluente del río Putumayo, correg. la Chorrera, *J. Gasche 1137* (US); Santa Isabel, *M. Pabon 684* (COAH, NY). **Boyacá:** carretera Aguazul–Yo-

pal, quebrada Blanca, 7 km de Aguazul, *C. Sastre 769* (US). **Caquetá:** 10 km al sur de Belen, 360 m, ene. 1974, *A. Gentry 9110* (MO); 13 km de florencia hacia El Doncello, *J. Luteyn 4907* (MO, NY); 9 km al SW de Fragua, *A. Gentry 5730* (MO); Florencia, *E. Perez 710* (COL, US); San Vicente del Caguan, entre Campana y Puerto Majiña, *J. Betancur 2251* (HUA, MO); San Vicente del Caguan, Vda. el Recreo, Hato Varsovia, quebrada La Sal, *J. Betancur 1619* (HUA, MO). **Casanare:** Río Casanare, Esmeralda, *J. Cuatrecasas 3844* (US). **Cundinamarca:** Llano de San Martín, *J. Triana 692* (MO, P). **Meta:** Villavicencio, *T. Sprague 121* (F, US); Hato Horizontes, *J. Blydenstein 1061* (COL, MO, NY); 5 km de la via entre Villavicencio y Granada, *T. Croat 55530* (MO); llanos de San Martin Hoya del río Ariari, alrededores de la laguna Aguasucia, *R. Jaramillo 1136* (COL, US); sabanas de San Juan de Arama, río Guejar, *J. Idrobo 593* (COL, MO); Sierra de la Macarena, Río Guapaya, *W. Philipson 1583* (US); Sierra de la Macarena, unión de los ríos Sansa y Guejar, *J. Idrobo 2043* (COL, NY); Valle del Río Guayariba, 15 km O de Villavicencio, *M. Grant 9942* (MO); Villa de Concepción, 14 km E de Villavicencio, *J. Luteyn 4754* (MO, NY). **Nariño:** Cananguchо, 162 km E de Pasto, *R. Espinosa 3049* (NY). **Putumayo:** entre Mocoa y Urcusique, quebrada Obandoyaco, *Ewan 16791* (MO, US); frontera Colombo–Ecuatoriana, Río San Miguel, entre los afluentes Bermeja y Conejo, *J. Cuatrecasas 11055* (US); Mocoa & vic., *R. Schultes 19044* (NY, US); Puerto Ospina, Río Putumayo, *J. Cuatrecasas 10861* (US); Umbria, *C. Klug 1663* (MO, NY). **Vaupés:** Mitu y alrededores, *R. Schultes 13975* (COL, NY, US); Río Piraparana, tributario del río Apoporis, Caño Teemeeña, *R. Schultes 17452* (US); Río Vaupes, entre Mitu y Javarete, cerro Tipiaca, *R. Schultes 19323* (GH, MO); Río Vaupes, entre Mitu y Javarete, desembocadura de Querari, *R. Schultes 19340* (US); Riveras del Río Inirida, Raudal Alto, cerro el Varador, *A. Fernandez 2091* (COL, US). **Vichada:** 8 km al E de Las Gaviotas, *G. Davidse 5169* (MO); borde del Río Vichada, San José de Ocuné, *J. Hermann 11052* (US).

2. Spathiphyllum laeve Engl., Bot. Jahrb. 37: 120. 1905. TYPE: Costa Rica. "Commune dans les bois, Vallée Gissler, Ile Cocos, Pacifique," 18 June 1898, *H. Pittier 12370* (holotype, B; isotype, US not seen).

Spathiphyllum laeve was until recently only known from Isla de Cocos in Costa Rica. However, a large number of collections of this taxon has been made in the last decades from Nicaragua, Panama, and Colombia, where it is restricted to the northeastern border adjacent to Panama in the states of Antioquia and Chocó. *Spathiphyllum laeve* is rather common in shaded sites in the understory of humid forests on clay soils. It is the only known species of *Spathiphyllum* sect. *Massowia* that occurs in Mesoamerica and Colombia.

Spathiphyllum laeve grows from 0 to 900 m elevation in tropical wet forest life zones. Flowering collections in Colombia have been made in January, February, July, and October.

Representative specimens examined. COLOMBIA **Chocó:** E side, Serranía del Darien, from Acandi, along Guati river, *A. Juncosa 607* (MO); Nuqui, correg. Termales, *J. Betancur 6016* (COL); Riosucio, Cerros del Cuchillo, *D. Cardenas 1348* (JAUM); trail from Río Tigre base camp up Serranía del Darien W of Ungía, *A. Gentry 15239* (MO).

COSTA RICA. **Alajuela:** Res. Monteverde, Poco Sol 13 km S Fortuna, *W. Haber 9349* (CR, MO); 15 km NW of Arenal by air, *R. Liesner 15110* (MO); ca. 1 km SE of La Balsa de San Ramón, *M. Grayum 6352* (MO). **Cocos Island:** Wafer Valley, *L. Gomez 3286* (MO); near Wafer Bay, *R. Dressler 4465* (MO). **Heredia:** "Starkey woods," across river Puerto Viejo, *R. Dressler 4679* (MO); N base of hills to S of Río Sarapiqui, opposite Chilamate, *M. Grayum 5314* (MO). **Puntarenas:** along road betw. palmar Norte & Panamerican border, 3 km N of turn-off Rincón, *T. B. Croat 79187* (MO).

II. **Spathiphyllum** sect. **Amomophyllum** (Engl.) Engl., in DC., Monogr. Phan. 3: 227. 1879. TYPE: *Spathiphyllum gardneri* Schott.

KEY TO THE SPECIES OF *SPATHIPHYLLUM* SECT. *AMOMOPHYLLUM* IN COLOMBIA

1a. Leaf blade 3.5–9 times longer than wide.
  2a. Primary lateral veins arising at 11–30°.
    3a. Geniculum 2–3 cm long, spadix 4–6.4 cm long ..... 1. *S. quindiuense*
    3b. Geniculum 0.8–1 cm long, spadix 1.3–3 cm long ..... 2. *S. schomburgkii*
  2b. Primary lateral veins arising at 35–70°.
    4a. Leaf blade ovate-lanceolate, base obtuse; Amazonas ..... 3. *S. tenerum*
    4b. Leaf blade narrowly elliptic to oblong; Amazonas or interandean valleys.
      5a. Plants shorter than 30 cm; Amazonas ..... 4. *S. minor*
      5b. Plants taller than 35 cm; interandean valleys ..... 5. *S. patinii*
1b. Leaf blade 2–3 times longer than wide.
  6a. Primary lateral veins arising at 45° ..... 6. *S. kalbreyeri*
  6b. Primary lateral veins arising at 55–70°.
    7a. Petiole as long as the leaf blade.
      8a. Leaf blade ovate-elliptic ..... 7. *S. perezii*
      8b. Leaf blade oblanceolate to elliptic-oblong .... 8. *S. floribundum*
    7b. Petiole 1.3–2 times longer than the leaf blade.
      9a. Geniculum 2–3.5 cm long ..... 9. *S. fulvovirens*
      9b. Geniculum 0.5–1.7 cm long.
        10a. Spathe decurrent to the peduncle 0.4–1.4 cm ..... 10. *S. silvicola*
        10b. Spathe free or inconspicuously decurrent ..... 7. *S. perezii*

1. Spathiphyllum quindiuense Engl., Bot. Jahrb. Syst. 37(1): 120. 1905. TYPE: Colombia. Quindío: 1000 m, *Triana 693* (holotype, BM not seen).

Spathiphyllum quindiuense was first collected by the Colombian botanist J. J. Triana from Quindío (no further locality was specified). Additional collections from Colombia were made by Castañeda in 1954 at Barrancabermeja along the Río Magdalena and by F. C. Lehmann in 1891 in the southeastern portion of Antioquia in the municipio of Nariño. Bunting (1960) reported the species as having been collected in Panama by Seibert. Additional collections of *S. quinduense* from Puerto Berrio in the Río Magdalena valley were made in 1990 by R. Callejas, who also collected the species in the tributaries of the Río Cauca in the Central Cordillera in Colombia.

Spathiphyllum quindiuense is known from tropical wet forest life zones at 200 to 1400 m elevation; flowering possibly occurs all year round.

Representative specimens examined. COLOMBIA. **Antioquia:** Remedios, 14–17 km de la vía Remedios–Zaragoza, región del cerro Cabeza, *R. Callejas 5159* (HUA); Amalfí, km 15–35, en la vía de las veredas Chorritos–Los Monos, *Callejas 9040* (HUA, MO); Caceres, Cabecera municipal el 12, Bajo Cauca, entre las quebradas Purí y Corrales, *Callejas 227* (HUA); Nariño, Río San Pedro, *Lehmann 7590* (US); Puerto Berrio, vereda Alicante, Finca Penjamo, 1 km al S de la finca, *R. Callejas 9246* (HUA, NY); Puerto Berrio, vereda Bodegas, sitio San Juan de Bedout, quebrada San Juan, *R. Callejas 9341* (HUA); San Carlos, corr. alto Samana, vereda el Silencio–Jardin, *R. Callejas 8523* (HUA, MO); San Luis, Río Dormilón, Charco La Cascada, *S. Hoyos 93* (HUA); San Luis, Vereda Manizales, a orillas del Río Dormilón, *C. Orozco 616* (COL); Zaragoza, Trayecto Río Tiguí a Zaragoza, *R. Callejas 4621* (HUA).

2. Spathiphyllum schomburgkii Schott, Oesterr. Bot. Wochenbl. 7: 158. 1857. TYPE: Venezuela. "1st Coll. M. Roraima," *R. H. Schomburgk s.n.* (holotype, K not seen).

Spathiphyllum schomburgkii was made a variety of *Spathiphyllum candolleanum* by Engler (1879) based on the nature of the pistil; however, after a considerable examination of the pistil, Bunting (1960) did not accept the varietal status.

Spathiphyllum schomburgkii was initially known to be restricted to Mount Roraima in Venezuelan territory; a careful examination of herbarium collections at HUA revealed in Colombia at least two disjunct populations of this taxon, both in northeastern Colombia, one at the Magdalena valley (state of Santander) and a second population at the northern extreme of the Río Cauca canyon near the town of Tarazá (Antioquia). The species appears to be restricted to the margins of water streams in shadowy places, and it can be recognized by the low stature of the plants (0.35 m), the length of the petiole (equal to or less than the lamina length), and by the leaves narrowly elliptic, 4–6 times longer than wide.

Spathiphyllum schomburgkii grows in tropical wet forest life zones at 100 to 500 m elevation. Flowering collections have been made in August and September.

Representative specimens examined. COLOMBIA. **Antioquia:** Taraza, corr. El Doce, en camino a Barroblanco, *R. Callejas, S. Churchill et al. 2397* (HUA, NY). **Santander:** vic. Barrancabermeja, Magdalena Valley, betw. Sogamoso & Colorado Rivers, *O. Haught 1367* (US).

3. Spathiphyllum tenerum Engl., Bot. Jahrb. 37: 120. 1905. TYPE: Peru. Loreto: "Bodenpfl., Bl. grunlich weeiss, Cerro de Ponasa, 1200 m," Feb. 1903, *E. Ule 6851* (holotype, B!; isotypes, G-DEL not seen, MG not seen).

Spathiphyllum tenerum exhibits leaves that are ovate-lanceolate (4 times longer than wide) and secondary veins that diverge from the midvein in angles of 70°. The species was first described by Engler in 1905 from Cerro Ponasa in the province of Loreto (Peru) at a rather unusually high elevation for the genus (1200 m). A second collection is known from the department of Amazonas in Colombia but at much lower elevation (200 m).

Representative specimen examined. COLOMBIA. **Amazonas:** corr. Tarapaca, vereda El Porvenir, *R. Lopez et al. 4375* (COAH).

4. Spathiphyllum minor G. S. Bunting, Mem. New York Bot. Gard. 10(3): 31. 1960. TYPE: Peru. Junín: Pichis Trail, Santa Rosa, 625–900 m, 6, 7 July 1929, *E. Killip & A. Smith 26153* (holotype, US!; isotype, NY!).

Spathiphyllum minor, originally described by Bunting (1960) from Junín (Peru), has been collected in Colombia in the southern state of Amazonas near the border with Peru. This species is noted for its small size (0.3 m), the soft leaf texture, and the rather short stipe.

Spathiphyllum minor is found at 200–300 m elevation in tropical wet forest. Flowering occurs in January, March, July, and September.

Representative specimens examined. COLOMBIA. **Amazonas**: Leticia, Río Tacana, *3 c 114* (HUA); Puerto Nariño, *G. Lozano, F. Patiño & V. Romero 618* (COL); Leticia, Inspección de policía Calderon, *R. Lopez, Augusto Mazorra & Jose L. Marmoz 5889* (COAH); corr. Tarapaca, *R. Lopez, D. Cardenas et al. 5022* (COAH).

5. Spathiphyllum patinii (Hogg) N. E. Br., Gard. Chron. 2: 783. 1878. *Anthurium patini* Hogg, Gard. Year Book 123. 1875. TYPE: Colombia.

Antioquia: Gomez Plata, cuenca del río Porce, hacienda Vegas de La Clara, 950 m, 6°37′00″N, 75°15′00″W, ago. 2003, *F. Cardona, R. Callejas et al. 1171* (neotype, designated here, HUA!; isotype, MO!).

This species was first mentioned as *Anthurium patini* in the *Garden Year Book*, by Hogg (1875) and in *Garden Chronicles* by Masters (1875) without any formal description but accompanied by a single illustration. Afterward, N. E. Brown (1878), in clear reference to Master's illustration, transferred *A. patinii* to the genus *Spathiphyllum*.

Since the original collection and Bunting's treatment in 1960, specimens collected in Colombia that agree with the original description come from the northern Magdalena valley in Antioquia near the municipios of San Luis and San Carlos, where the plants grow on rocky granitic outcrops. It is worth noting that this region includes many endemic species of angiosperms first described in Europe from horticultural catalogs. In fact, the area of San Carlos was very much traveled in the 19th century by European plant collectors, as it was the route for entering Antioquia from the Río Magdalena. At the present time, *Spathiphyllum patinii* seems to be restricted to a narrow corridor in the Magdalena valley and to a disjunct population in the Río Anorí, a tributary of the Río Cauca in Antioquia.

Spathiphyllum patinii ranges from 300 to 1400 m elevation in tropical wet forest and premontane wet forest life zones. Flowering collections have been made in most parts of the year.

Representative specimens examined. COLOMBIA. 1760–1808, *J. S. Mutis 1123* (MA, US). **Antioquia:** "Río Claro, along hwy. between Pto. Triunfo and Medellín," *T. Croat 56547* (MO); San Carlos, "creek affluent to rio Guatape, ca. 1.5 km from presa Punchina," *M. Grayum 7612* (MO); Amalfi, 8–27 km EN de Amalfi, en la via Vetilla–Fraguas, *R. Callejas 9146* (HUA, MO); Maceo, Vereda Santa Barbara, quebradas Guardasol y Alicante, *F. Cardona & Carlos Lopez 1085* (HUA); Puerto Berrio, La Carlota, quebrada El Vapor, *F. Cardona, A. Idarraga & J. Benavides 1067* (HUA).

6. Spathiphyllum kalbreyeri G. S. Bunting, Mem. New York Bot. Gard. 3: 21, f. 5. 1960. TYPE: Colombia. Rastrojas, 3000 ft., 15 Feb. 1880, *W. Kalbreyer 1413* (holotype, K not seen).

Since the original collections of *Spathiphyllum kalbreyeri*, six collections have been made, two by Hutchison in 1905 and O. Haught in 1936, and four by the author in Antioquia. *Spathiphyllum kalbreyeri* is known in Colombia from the Río Magdalena valley at 100 to 500 m elevation in tropical wet forest life zones.

Representative specimens examined. COLOMBIA. **Santander:** vic. Barrancabermeja, Magdalena valley, betw. Sogamoso & Carare Rivers, alt. 100–500 m, 1 July 1936, *O. Haught 1894* (US). **Caldas:** La Dorada, río de la Miel, *Hutchison 3194* (US). **Antioquia:** Maceo, Vereda Santa Barbara, quebradas Guardasol y Alicante, *F. Cardona & Carlos Lopez 1085* (HUA); Puerto Berrio, La Carlota, quebrada El Vapor, *F. Cardona, A. Idarraga & J. Benavides 1067* (HUA); Taraza, corregimiento El Doce, quebrada Puri, *F. Cardona, R. Callejas et al. 1049* (HUA); Valdivia, corregimiento Puerto Valdivia, cuenca del rio Pescado, *F. Cardona, R. Callejas & Carolina Robles 1078* (HUA).

7. Spathiphyllum perezii G. S. Bunting, Acta Bot. Venez. 10: 321. 1975. TYPE: Venezuela. Mérida: carretera El Vigia–San Cristóbal de Táchira, 9 km al suroeste del Vigia, entre el Vigia y el Quince, en barranca silvestre, alt. ca. 125 m, 3 Oct. 1967, *G. S. Bunting 2405* (holotype, MY not seen).

Spathiphyllum perezii is here reported as new to Colombia. The type of this species comes from the state of Mérida in Venezuela, collected by Bunting in 1967. This taxon was first found in Colombia by Ramírez in 1987 and Grayum in 1986, both in the Antioquia department near the Magdalena valley.

Spathiphyllum perezii ranges from 500 to 1500 m elevation in tropical wet forest life zones. Flowering collections in Colombia have been made in May, July, and September.

Representative specimens examined. COLOMBIA. **Antioquia:** San Luis, quebrada la Cristalina, *J. Ramírez 1754* (JAUM, MO); San Carlos, "primary forest along quebrada La Negra, tributary to Punchiná reservoir, Río Guatape,"*M. Grayum 7628* (MO).

8. Spathiphyllum floribundum (Linden & André) N. E. Br., Gard. Chron. 2: 783. 1878. *Anthurium floribundum* Linden & André, Ill. Hort. 22, t. 159. 187. TYPE: Colombia. Antioquia: San Carlos, correg. El Jordan, vda. Juanes, 230 m, Mar. 1988, *L. Albert 8324* (neotype, designated here, HUA!; isotypes, MO!, NY!).

This species was first mentioned as *Anthurium floribundum* in *L'Illustration Horticole* by Linden and André (1874). In Colombia many populations of *Spathiphyllum floribundum* occur in the Cauca valley in northern Antioquia and Río Magdalena valley, where it appears to be a rather common element of forest streams. It is sympatric with *S. fulvovirens*.

Spathiphyllum floribundum grows in tropical rain

forest life zones, from 200 to 1500 m elevation. Flowering collections have been made throughout the year.

Representative specimens examined. COLOMBIA. **Antioquia:** San Carlos, lake Punchina, *A. Brant 1660* (HUA, MO, US); Amalfi, near Salazar, *J. MacDougal 3992* (MO); Amalfi, sitios Zalazar y Marengo, via Vetilla Fraguas, *R. Callejas 9146* (HUA, NY); Anori, El Río y Bramadero, *R. Callejas 8715* (HUA, MO, NY); San Carlos, ca. 1.5 km from presa Punchina, *M. Grayum 7613* (MO); San Carlos, corr. Alto Samana "Vda. Miraflores," quebrada Miranda, *R. Fonnegra 2976* (HUA, MO, NY); San Carlos, ISA hydroelectric dam reservoir, *G. McPherson 13336* (MO); San Luis "Quebrada la Cristalina," *J. Ramírez 1926* (JAUM, MO); San Luis, Cañón del Río Claro, *A. Cogollo 1142* (JAUM, MO); San Luis, Piedra de Castrillon, *D. Daly 5887* (HUA, MO, NY); San Luis, río Samana Norte, *R. Callejas 4083* (HUA, MO); San Luis, sector río Samana, *J. Hernandez 187* (HUA, NY); San Luis, Vda. la Josefina, camino a Palmita, *S. Hoyos 469* (JAUM, MO); San Luis, Vda. las Confusas, *D. Cardenas 2669* (JAUM, MO); Taraza, correg. El Doce, *R. Callejas 2411* (HUA, MO); Río Nuz, *Lehmann 7758* (F, US); Sabaleta, *Lehmann 7757* (F). **Boyacá:** El Humbo, *A. Lawrance 696* (F, MO, US). **Caldas:** Río Samana, Caldas, *A. Barkley 35352* (US). **Córdoba:** Tierralta, quebrada afluente del Río Simi, *R. Bernal 1191* (COL, MO). **Cundinamarca:** Paime, *Bro. Ariste-Joseph A924* (US). **Santander:** Magdalena Valley, Campo Capote, *A. Gentry 20037* (MO); vic. Barrancabermeja, betw. Sogamoso & Colorado rivers, *O. Haught 1386* (US).

9. Spathiphyllum fulvovirens Schott, Oesterr. Bot. Z. 8: 179. 1858. TYPE: Panama. Bocas del Toro: vicinity of Chiriquí Lagoon, fish Creek, 9 Apr. 1941, *H. von Wedel 2198* (neotype, designated by G. S. Bunting (1960: 27), GH not seen; isotypes, F not seen, MO!).

Common in Costa Rica and Panama, *Spathiphyllum fulvovirens* is also known from Colombia, where it occurs in the northern portion of the Río Magdalena valley, along the Pacific in Chocó and Valle del Cauca and in the Amazonian states of Caquetá and Putumayo. Bunting (1960) indicated that the disjunct population in Colombia differs from those in Central America in having narrower leaf blades. Since his treatment, collections of this species by Croat from Valle department and Cárdenas in Pto. Berrio not only confirm Bunting's observation, but also seem to indicate a disjunct distribution pattern for the species.

Spathiphyllum fulvovirens in Colombia occurs at 200 to 1100 m elevation in tropical rain florest and tropical wet forest life zones.

Representative specimens examined. COLOMBIA. **Antioquia:** Puerto Nare, vda. Serranias, *D. Cardenas 3018* (JAUM); Taraza, corr. el Doce, Vda. Barroblanco, quebrada Puri, *R. Callejas 3627* (HUA); Amalfi, 8–15 km de Amalfi a Rumazón, sitios Salazar y la Playa, *J. Betancur 787* (HUA); San Luis, Parque Ecológico El Castellon, *F. Alzate 702* (HUA); San Luis, Vda. Manizales, *R. Callejas 4315* (HUA); Turbo, carr. tapon del Darién, sector Río Leon-Lomas Aisladas, km 36, *J. Brand 795* (JAUM, MO); selva veranera cerca de Porcesito, en el valle del Río Medellín, *W. Hodge 6870* (US). **Caquetá:** 13 km SE de Morelia along road to Río Pescado (SW of Florencia), *G. Davidse 5680* (MO). **Chocó:** Río Truando, *J. Duke 13307* (NY); rain forest on hill N of alto Curiche, *J. Duke 11219* (NY); via entre San Jose del Palmar y Novita, 3 km W de San Jose del Palmar, *T. Croat 56646* (MO). **Putumayo:** Pto. Porvenir, selva higrofilica del Río Putumayo, arriba de Puerto Ospina, *J. Cuatrecasas 10665* (COL). **Santander:** vic. Barrancabermeja, Magdalena Valley, betw. Sogamoso & Carare Rivers, Amarilla Creek, *O. Haught 1895* (US). **Valle del Cauca:** from Queremal to Buenaventura, along Río Ningaño, *T. Croat 79724* (MO).

10. Spathiphyllum silvicola R. A. Baker, Phytologia 33: 448. 1976. TYPE: Costa Rica. Puntarenas: canton de Osa, forest near Esquinas Exp. study area betw. Río Esquinas & Palmar de Osa, 200 ft., 3 Oct. 1967, *P. H. Allen 5538* (holotype, F!; isotypes, CR!, IAP not seen, US not seen).

Spathiphyllum silvicola is quite similar to *S. laeve* in laminar shape and general appearance. Both species can be distinguished rather easily, however, by the apically free perianth segments of *S. silvicola* that are not united as in *S. laeve*.

Spathiphyllum silvicola ranges from the Chocó lowlands along the northern Pacific Coast in Colombia to the province of Puntarenas in Costa Rica.

Spathiphyllum silvicola grows in tropical rain forest and tropical wet forest life zones at 20 to 500 m elevation. Flowering collections have been made in January, February, July, September, October, and December.

Representative specimens examined. COLOMBIA. **Antioquia:** Turbo, carr. Tapon del Darien, km 36, *J. Brand 795* (JAUM); Turbo, Corr. Lomas Aisladas, *E. Renteria 3500* (JAUM, MO). **Chocó:** Parque Nac. Nat. Los Katios, zona del alto de La Guillermina, *S. Zuluaga 1113* (COL).

Another species in section *Amomophyllum*, *Spathiphyllum neblinae*, is reported as occurring in Colombia (Bunting, 1960). However, after examining the collection of *Schultes & Cabrera 15824* (MO), I am convinced that it has to be referred to a new species, at least based on its decurrent spathe and short stipe, but more collections are needed to confirm it as such. The *Schultes & Cabrera* collection was made in 1952 near the Miriti–Parana River, a tributary of the Río Caquetá.

III. Spathiphyllum sect. **Dysspathiphyllum** Engl., Pflanzenreich 4: 120. 1908. TYPE: *Spathiphyllum humboldtii* Schott.

Spathiphyllum sect. *Dysspathiphyllum* includes the single species *S. humboldtii*, which has the distinctive feature of a blunt pistil apex.

1. **Spathiphyllum humboldtii** Schott, Aroideae 1: 2. 1853. TYPE: "Surinam." *F. W. Hostmann 1154* (lectotype, designated by Bunting (1960: 33), K not seen; isotypes, BM not seen, G-DEL!, U not seen).

The only species of section *Dysspathiphyllum*, *Spathiphyllum humboldtii* is widespread in eastern Amazonia and northeastern South America, where it occurs from Surinam through Venezuela, French Guiana, Brazil, Ecuador, and Peru. In Colombia, it has been collected at Tuparro in the eastern part of the country.

Spathiphyllum humboldtii in Colombia grows at 100 to 300 m elevation in tropical wet forest life zones. Flowering collections have been made in March.

Representative specimens examined. COLOMBIA. **Vichada:** territorio faunístico del Tuparro, 4 km NW of the headwaters of caño Peinillas, 160 m, Mar. 1980, *P. Vincelli 1280* (COL, MO).

IV. Spathiphyllum sect. **Spathiphyllum** Bunting, Mem. New York Bot. Gard. 10: 34. 1960. TYPE: *Spathiphyllum lancaefolium* (Jacq.) Schott.

KEY TO THE SPECIES OF *SPATHIPHYLLUM* SECT. *SPATHIPHYLLUM* IN COLOMBIA

1a. Leaf blade 1.5–2 times longer than wide.
  2a. Base obtuse or rounded ..... 1. *S. grandifolium*
  2b. Base acute ..... 2. *S. friedrichsthalii*
1b. Leaf blade 2.5–3 times longer than wide.
  3a. Pistil exceeding the perianth by 0.3–0.4 cm, cylindrical and rounded at the apex ..... 2. *S. friedrichsthalii*
  3b. Pistil exceeding the perianth by 0.1–0.2 cm, attenuate-conic.
    4a. Leaf blade lanceolate, acute or sometimes obtuse at the base .... 3. *S. zetekianum*
    4b. Leaf blade oblong-lanceolate or elliptic-oblong, rounded, truncate or obtuse at the base.
      5a. Peduncle 1.4–1.7 times longer than the petiole ..... 4. *S. lancaefolium*
      5b. Peduncle 0.6–1.1 times longer than the petiole ..... 5. *S. phryniifolium*

1. **Spathiphyllum grandifolium** Engl., Bot. Jahrb. Syst. 37: 119. 1905. TYPE: Colombia. Nariño: "auf dem Boden in dichten Regenwäldern bei Altaquer an den Westabhängen das Cordilleren von Pasto, 1000 m," 12 Mar. 1881, *F. C. Lehmann 563* (holotype, B!).

This species was known until 1988 only from the type locality in the Cordillera Occidental in Nariño Department, where it was collected by the German orchid and gold mining entreprenuer F. C. Lehmann in 1881. Working in Nariño during 1988, B. Hammel collected this species once again, and in 1996 Silverstone-Sopkin extended its range of distribution to Risaralda along the Cordillera Central in northwestern Colombia.

Spathiphyllum grandifolium ranges from 900 to 1000 m elevation in tropical wet forest life zones. Flowering collections have been made in March, May, November, and December.

Representative specimens examined. COLOMBIA. **Nariño:** via El Espino–Tumaco, 30 km W de Ricaurte, El Mirador, finca Santa Lucia, *B. Hammel 17181* (MO). **Risaralda:** Hacienda Alejandria, km 6 carr. Virginia–Cerrito, valle del Río Cauca, *P. Silverstone 5297* (CUVC, MO), dic. 1995, *P. Silverstone 7441* (CUVC, MO).

2. **Spathiphyllum friedrichsthalii** Schott, Aroideae 1: 2. 1853. TYPE: Costa Rica. Limón: "in Gynaerium sagittatum thickets along Río Reventazón below farmhouse, Finca Castilla," 30 m, 27 July 1936, *C. W. Dodge & V. F. Goerger 9414* (neotype, designated by Bunting (1960: 35), F; isotype, MO not seen).

Engler described three varieties, two in 1879 (var. *angustifolium* and var. *latifolium*) and one in 1907 (var. *brevifolium*); however, these could be geographical variations of the same species.

Spathiphyllum friedrichsthalii is the most widespread of the four species known in Colombia from section *Spathiphyllum*. It occurs in the Chocó region from the Darién in the north to the Colombian border with Ecuador in the south. The species often grows in large populations along streams and was the subject of reproductive biology studies (Montalvo & Ackerman, 1986). This species has been introduced in the local horticultural market in Colombia and is often seen as a house plant.

Spathiphyllum friedrichsthalii is known from tropical rain forest and tropical wet forest life zones. Flowering collections have been made throughout the year.

Representative specimens examined. COLOMBIA. **Antioquia:** 18 km al sur de Chigorodo, *M. Palacio 104* (HUA, MO, NY); Chigorodo, 23–27 km NW de Chigorodo, *R. Callejas 9712* (HUA); near Guapá, 53 km S of Turbo, *O. Haught 4598* (US); Uraba, entre Mutata y Pavarandocito, *L. Uribe 2038* (COL, NY); Villa Arteaga, *C. Brahe 18C701* (US). **Cauca:** costa del Pacífico, Río Micay, Noanamito, *J. Cuatrecasas 14217* (US). **Chocó:** 26 km S de Quibdo, across river from Yuto, *A. Gentry 23750* (HUA); alrededores de Quibdo, *J. Araque 19CH049* (US); Andagoya, *Killip 35076* (US); Baudo, river Baudo, quebrada

Majagual, *H. Fuchs 1501* (US); camino entre Playas de Oro y Tado, *T. Croat 80763* (MO); carr. Istmina, 10 km antes de Yuto, *J. Santa 278* (HUA); Hoya del río San Juan, Río Bocordó, alrededores de Noanamá, *E. Forero 4650* (COL, HUA); Jurubidá, playa Peñas Blancas, quebrada Aguas Calientes, *A. Gomez 316* (HUA); Riosucio, cerros del cuchillo, *D. Cardenas 1386* (JAUM, MO); Pizarro, carr. Pepe–Berrecul km 21, *J. Espina 1937* (Chocó, MO); Riosucio, cerros del cuchillo, *D. Cardenas 1895* (JAUM, MO); Río Atrato, 2–5 hours below Río Sucio, above Loma Teguerre, *J. Duke 11003* (US); Río Serrano, 4–6 km arriba de Guayabal, *E. Forero 1388* (COL, MO); Río Truando, *Schott 3* (NY); Trocha Utria al Valle, Costa Pacífica, *A. Fernandez 273* (COL, US). **Córdoba:** Dagua Valley, *Killip 5034* (NY, US). **Nariño:** Isla de Gallos, Pacífico, *E. Dryander 2589* (US); Rives du Río Mira, *E. Langlassé 2* (US). **Valle:** Córdoba, *Killip 33397* (US); Río Calima, La Trojita, *J. Cuatrecasas 16366* (US); Río Dagua, Buenaventura, *Lehmann 5361* (NY); Río Raposo, Raposo field station, *M. Bristol 700* (US); Sabaletas, km 29, hwy. from Buenaventura to Cali, *Killip 38859* (US).

3. Spathiphyllum zetekianum Standl., Ann. Missouri Bot. Gard. 27: 267. 1940. TYPE: Panama. Barro Colorado island, canal zone, July 1931, *D. E. Starry 27* (holotype, F, photo F-051251!).

Spathiphyllum zetekianum is found along the western slopes of the Western Cordillera to the Pacific lowlands of Chocó and neighboring Panama. As with many other species of the genus, this appears to be restricted to the forest interior and associated with sandy or clay soils. It grows at 0 to 600 m elevation in tropical wet forest. Flowering collections have been made in January, April, and July.

Representative specimens examined. COLOMBIA. **Chocó:** Acandi, corr. Sapzurro, *MEDEL 100* (MEDEL); Nuqui, Corr. Arusí, est. biol. El Amargal, *Jorge Jacome 314* (COL, HUA); Unguía, resguardo de Arquía, *Giraldo, Izquierdo & Pinto 45GIP* (COL); Carmen de Atrato, carr. entre el Carmen y Quibdo, *F. Cardona, R. Callejas et al. 1018* (HUA).

4. Spathiphyllum lancaefolium (Jacq.) Schott, Melet. Bot. 22. 1832. *Dracontium lanceaefolium* Jacq., Coll. Nom. Broth. 4: 118. TYPE: Jacquin, Ic. Pl. Rar. 3: pl. 612 (1786–1793).

Spathiphyllum lancaefolium is likely the most common and locally abundant species of the genus occurring in the mid and upper Magdalena valley of Colombia, but its presence in Colombia remained undetected since it was first described by Engler and Krause from neighboring Venezuela in 1908. Individual plants of this species attain heights of almost 2 m and are a frequent component of the forest interior, in areas either commonly or occasionally flooded. The species grows at 100 to 600 m elevation in tropical wet forest life zones. Flowering collections have been made from July to October.

Representative specimens examined. COLOMBIA. **Antioquia:** Puerto Berrio, caño a 4 km de San Juan de Bedout, en la via a Yondo, *F. Cardona & R. Callejas 1112* (HUA); San Luis, cañon del río Claro, *F. Cardona et al. 1189* (HUA); San Luis, alrededores de la Vereda Chorro de Oro, *A. Cogollo et al. 4592* (JAUM). **Caldas:** Norcasia, proyecto hidroeléctrico La Miel, *W. Vargas 6335* (HUA). **Cundinamarca:** Caparrapí, *H. Garcia B. 7676* (COL). **Quindio:** La balsa, from Ibagué to Toche, 1844, *Goudot s.n.* (MO). **Santander:** Cimitarra, 5 km despues de cruzar el puente sobre el Río Magdalena desde Puerto Berrio, hacienda El Bosque, *F. Cardona & Carlos Lopez 1090* (HUA); Cimitarra, potrero quito, *J. Perez et al. 1096* (HUA, JAUM). **Tolima:** Mariquita, bosque de la res. mun., *L. González 17* (COL); Venadillo, vda. San Antonio, *J. Idrobo 10731* (COL); Venadillo, Vda. Berlina, *J. Idrobo 10765* (COL).

5. Spathiphyllum phryniifolium Schott, Oesterr. Bot. Wochenbl. 7(20): 159. 1857. TYPE: Panama. "Chagres, Isthmus of Panama," mouth of the Río Chagres, canal zone, Jan. 1850, *A. Fendler 425* (holotype, K not seen).

Spathiphyllum phryniifolium is known from Panama, Costa Rica, and Colombia. In Colombia it has been collected (1976) in the northwestern portion of the Chocó region along the border with Panama by E. Forero, and more recently (1990) in Salgar, department of Antioquia near Chocó, by T. Croat. *Spathiphyllum phryniifolium* grows at 50 to 100 m elevation in tropical rain forest and tropical wet forest life zones. Flowering collections have been made in February, March, November, and December.

Representative specimens examined. COLOMBIA. **Chocó:** Acandí, Unguia y alrededores, *E. Forero 1986* (COL). **Antioquia:** Salgar, *T. Croat 69892* (MO).

Discussion

While collecting *Spathiphyllum* in Colombia, one soon discovers that a strong ecological component exists in species distribution, where substrate preferences along watersheds are specific for many species. Some species of *Spathiphyllum* prefer shady sites and soils with sandy substrates along watercourses (cf. *S. floribundum, S. friedrichsthalii, S. cannifolium*) that are not subject to periodical flooding. On the other hand, species like *S. patinii* prefer the exposed rock crevices along streams. *Spathiphyllum quindiuense* prefers rocks on streambeds in fully exposed sites where the rhizomes are always fully covered by water.

The genus *Spathiphyllum* exhibits distinct pat-

terns of distribution in Colombia, which can be summarized as follows:

It is evident that a considerable number of species in the genus occur in or are restricted to the Magdalena valley (9), and that fewer species (6) are known from the Chocó region or Amazonia (5).

Nine species are known from the Magdalena valley, none of which is endemic; five of these species (*S. floribundum, S. quindiuense, S. kalbreyeri, S. patinii,* and *S. fulvovirens*) are known also from Panama (D'Arcy, 1987a, b). *Spathiphyllum lancaefolium, S. schomburgkii,* and *S. perezii* occur also in Venezuela, and *S. floribundum, S. fulvovirens,* and *S. quindiuense* have disjunct populations in Ecuador, Peru, and Panama.

Spathiphyllum humboldtii from the east of Colombia has been collected in Peru and Ecuador (Croat, 1999; Vásquez, 1997).

For southeastern Colombia, in the Amazonian basin, *Spathiphyllum cannifolium* exhibits a widespread distribution and is by far the most common species in that region. Other species such as *S. minor* and *S. tenerum* are present in that region but with one or few collections.

The genus *Spathiphyllum* is not documented as very diverse in the Chocó Biogeographical Region, with only six species known from the area. *Spathiphyllum friedrichsthalii* is widespread in Chocó, while *S. grandifolium, S. fulvovirens,* and *S. phryniifolium* are known from one or few localities.

Bunting (1960) documented the occurrence of 12 species of *Spathiphyllum* in Colombia (four excluded here: *S. neblinae, S. juninense, S. lechlerianum,* and *S. kochii*). Here I report 10 additional taxa across four sections in *Spathiphyllum*: *S. humboldtii* (sect. *Dysspathiphyllum*); *S. phryniifolium, S. lancaefolium, S. zetekianum* (sect. *Spathiphyllum*); *S. minor, S. perezii, S. schomburgkii, S. silvicola, S. tenerum* (sect. *Amomophyllum*); and *S. laeve* (sect. *Massowia*).

Spathiphyllum is almost completely absent north of the Andes in Colombia; no species of *Spathiphyllum* are known from the Caribbean coast of any states and, more surprisingly, none has been collected from the Sierra Nevada de Santa Marta, an area with lowland forests and extensive and rich river systems. Also noteworthy is the paucity of species documented for the Chocó, an area rich in *Anthurium* and other Araceae, but evidently poor for *Spathiphyllum.* The Andean region itself is by far the richest part of Colombia in species of *Spathiphyllum* in the interandean valleys.

It is likely that insufficient collecting in Amazonian Colombia and even in the Sierra Nevada de Santa Marta may explain the low number of *Spathiphyllum* species in these areas; however, Chocó and the Pacific coast in general had been intensively collected at least for Araceae by Croat and for general flora by Gentry. It is expected that further fieldwork may corroborate the preliminary results presented here.

Spathiphyllum species occur along river banks, on loose clay or sandy soils in shady areas. Such habitats are more common in the interandean valleys below 1300 m than on the rocky river banks of the Chocó region. More research on the ecology of the species and more extensive collecting, nevertheless, are necessary before a solid hypothesis can be formulated to explain the distribution of the genus in Colombia.

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Note added in proof

Since the manuscript was submitted in 1999 fieldwork in several areas of Colombia has revealed the presence of other species of *Spathiphyllum,* 9 of which are taxonomic novelties and are not included here. The total number of taxa for the country is now estimated to be 27 species.

ARACEAE FROM CENTRAL BRAZIL: COMMENTS ON THEIR DIVERSITY AND BIOGEOGRAPHY[1]

Eduardo G. Gonçalves[2]

ABSTRACT

Current knowledge about the diversity and biogeography of aroid taxa from central Brazil is here presented and discussed. For practical reasons, the study area was limited to the Cerrado phytogeographic province. In all, 18 genera and 64 species of Araceae were found naturally occurring in the studied area. The genera found were: *Philodendron* (23 species), *Anthurium* (11), *Xanthosoma* (7), *Dracontium* (3), *Monstera* (3), *Caladium* (2), *Dieffenbachia* (2), *Spathicarpa* (2), *Taccarum* (2), as well as *Asterostigma*, *Gearum*, *Heteropsis*, *Pistia*, *Rhodospatha*, *Scaphispatha*, *Spathiphyllum*, *Urospatha*, and *Zomicarpa* (1 species each). The Jaccard similarity index between aroid flora of the Cerrado province and the two main contiguous forested provinces (Mata Atlântica and Amazonia) was calculated for both genera and species. The values obtained show a closer similarity in species composition between the Cerrado and Amazonia (0.127) than between the Cerrado and Mata Atlântica (0.088). However, the generic similarity with Mata Atlântica (0.591) is higher than with Amazonia (0.414). Approximately 32% of the aroid species of central Brazil can be considered endemic to the Cerrado province; the only genus known to be endemic to the Cerrado is *Gearum*.

Key words: Araceae, biogeography, Brazil, Cerrado, savanna.

In recent years, Brazilian ecosystems have been intensively studied, and floristic inventories (especially at the family level) have flourished. However, most published Floras concern Amazonia or areas of the Atlantic coastal forest (Mata Atlântica). Only a few studies dealt with areas of central Brazil where the biodiversity still remains poorly known or even unknown. This state seems even worse in families (such as Araceae) that are known to be less diverse in central Brazil than they are in other areas. Groups like these have been overlooked for a long time.

Most of central Brazil lies inside the Cerrado phytogeographic province, and this circumscription of the Cerrado province establishes the scope of my investigations (Fig. 1). The Cerrado province is characterized by middle-altitude uplands, usually ranging from 300 to 1300 m, but occasionally from sea level (Eiten, 1972). The climate corresponds to Köppen's Aw category (rainy tropical), and there is a well-marked dry season that lasts up to 5 months (Eiten, 1994). The average rainfall ranges from 650 to 2000 mm/year (Assad, 1994). The main portion of the Cerrado province is covered by cerrado vegetation, a savanna-like formation that usually occurs on very poor soils, and its aroid diversity is not immediately apparent. However, according to Ribeiro and Walter (1998), approximately 15% of the Cerrado province consists of differing vegetation types where aroids can be found, namely: gallery forests, seasonal marshes, hyperseasonal savannas, dry forests, limestone outcrops, and montane vegetation (campos rupestres). The aroid flora in most of these areas is still poorly known, and some recent studies have shown a surprising number of new species (Gonçalves, 1997, 2000a, b, 2003a; Gonçalves & Mayo, 2000; Sakuragui & Mayo, 1997).

MATERIALS AND METHODS

Most data shown here were obtained during the initial and exploratory phase of the project "Biodiversidade do Bioma Cerrado." The geographic delimitation of the Cerrado phytogeographic province follows the data compiled by Ribeiro and Walter (1998). Despite the fact that there are some disjunct areas of cerrado vegetation forming islands within Amazonia as well as other phytogeographic provinces, e.g., Caatinga province, only the central contiguous cerrado area will be treated here. Field

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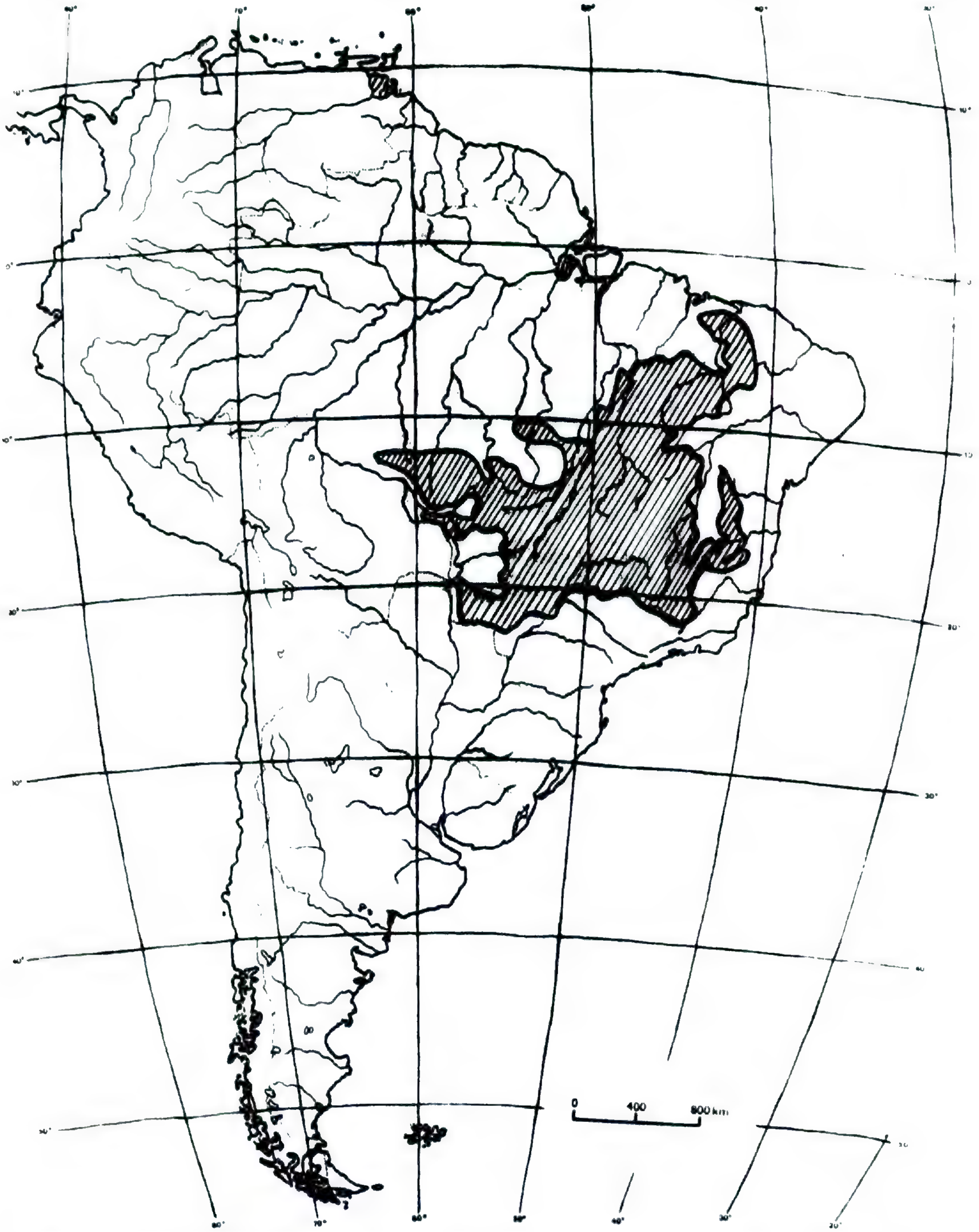

Figure 1. Central contiguous area of Cerrado phytogeographic province (adapted from Ribeiro & Walter, 1998).

trips were conducted from 1995 to 1999, mainly to areas where aroid collections were scanty. Dried specimens obtained from most herbaria inside the Cerrado province were also surveyed and mapped. The final report (including maps for all taxa) is still in preparation and should be published elsewhere (Gonçalves, Proença & Rosa, in prep.). In order to compare the cerrado vegetation with other biomes in Brazil, the preliminary checklist of Brazilian Araceae (Mayo et al., 1996, available from the author upon request) was used together with the checklist compiled by Govaertz and Frodin (2002). The data set was critically updated using the literature published after the last checklist (Gonçalves, 2003a, b,

c; Gonçalves & Temponi, 2004) and recently collected herbarium material. Comparisons between the aroid flora of the Cerrado and other phytogeographic provinces were made using the Jaccard index of similarity (Morrone et al., 1998). The index was calculated considering species as well as genera.

Results

THE CERRADO AS A MOSAIC OF FORMATIONS

A total of 18 genera and 64 species of Araceae was found occurring in the Cerrado province, and these are listed in Appendix 1. The most diverse genus is *Philodendron*, with 23 species, followed by *Anthurium* (11 species) and *Xanthosoma* (7 species). *Dracontium* and *Monstera* have three species each. *Caladium*, *Dieffenbachia*, *Spathicarpa*, and *Taccarum* have two species each. All the remaining genera (*Asterostigma*, *Gearum*, *Heteropsis*, *Pistia*, *Rhodospatha*, *Scaphispatha*, *Spathiphyllum*, *Urospatha*, and *Zomicarpa*) are represented in the Cerrado province by only one species each.

Although usually treated as a phytogeographic province, the Cerrado can be considered a mosaic of different formations, each one influenced by distinct environmental conditions as well as different paleoclimatic events. In order to present this complex framework, I decided to discuss each formation separately.

Cerrado (sensu stricto). This can be considered the "typical" structural type of the cerrado vegetation. It can be defined as a savanna woodland with scattered contorted trees and a ground layer of grasses, sedges, and occasional shrubs (Eiten, 1972). No species of Araceae were found growing in pure forms of this structural type, perhaps because the soils usually have high quantities of toxic aluminum (Goodland & Ferri, 1979).

Cerradão. This is considered a taller form of the cerrado type, usually occurring on slightly richer soils. Some terrestrial aroids can be found growing on these well-drained soils, mainly *Taccarum crassispathum* E. G. Gonç., *Scaphispatha gracilis* Brongn. ex Schott, and a still undescribed *Dracontium*. Climbers and hemiepiphytes are almost absent, except for the very occasional occurrence of *Philodendron wullshlaegelii* Schott.

Hydromorphic formations. These formations include permanent marshes, seasonal marshes, and hyperseasonal savannas. Permanent marshes have standing water throughout the year, and aroids like *Urospatha sagittifolia* (Rudge) Schott, *Philodendron uliginosum* Mayo, and a still undescribed species of *Dieffenbachia* usually grow there. Seasonal marshes have water above the soil surface during the rainy season, but it usually stays some centimeters below the soil surface during the dry season. *Xanthosoma striatipes* (Kunth) Madison usually occurs in this kind of marshy habitat. Hyperseasonal savannas are characterized by the alternation of extreme drought and flooding during the year (Sarmiento, 1983). In these savannas, *Gearum brasiliense* N. E. Br. and *Dracontium margaretae* Bogner can be found. Interestingly, both species from hyperseasonal savannas can be recognized by their linear leaflets.

Gallery forests. These formations usually occur along rivers and major streams. The gallery forests are usually treated as "corridors" of the Amazonian forests and of Mata Atlântica that extend inside the Cerrado province in a dendritic framework (Fernandes, 1998; Cabrera & Willink, 1973). Some aroids growing in this habitat are hemiepiphytes, such as *Philodendron guaraense* E. G. Gonç., *P. lundii* Warming, and *P. mello-barretoanum* G. M. Barroso. The delicate climber *P. guttiferum* Kunth is also common. Riparian aroids, e.g., *Spathiphyllum gardneri* Schott and *Xanthosoma riparium* E. G. Gonç., can be found growing on river banks. Although rheophytic aroids are not as common in the Neotropics as in the paleotropics, one of the few rheophytic species of *Philodendron* can be found in central Brazil. *Philodendron flumineum* E. G. Gonç. is common in rocks along fast-moving water (Gonçalves, 2000b). In fact, the vegetative convergence between such species of *Philodendron* and the Asian rheophytes (*Hottarum*, *Piptospatha*) is overwhelming, such as creeping stems firmly attached to the substrate and leathery leaves (lanceolate or long-elliptic) with a rostrate apex.

Mesophytic forest. Mesophytic forests (also known as dry forests) are usually found in restricted areas with well-drained and rich soils. This formation is often semideciduous (or even deciduous), and tuberous Araceae are common, namely *Xanthosoma plowmanii* Bogner, *X. syngoniifolium* Rubsy, an undescribed tuberous *Xanthosoma*, *Taccarum crassispathum*, *Asterostigma cryptostylum* Bogner, an undescribed *Caladium*, and *Spathicarpa gardneri*.

Limestone outcrops. These formations are usually rich in aroids, some of them growing directly on exposed rock (e.g., *Anthurium plowmanii* Croat and *A. affine* Schott). Other species are usually found growing in humus-filled crevices, often in the understory of deciduous forests. This group includes *Taccarum crassispathum*, *T. weddellianum* Brongn. ex Schott, *Spathicarpa gardneri*, and *Xanthosoma pentaphyllum* (Vell.) Engl. All tuberous

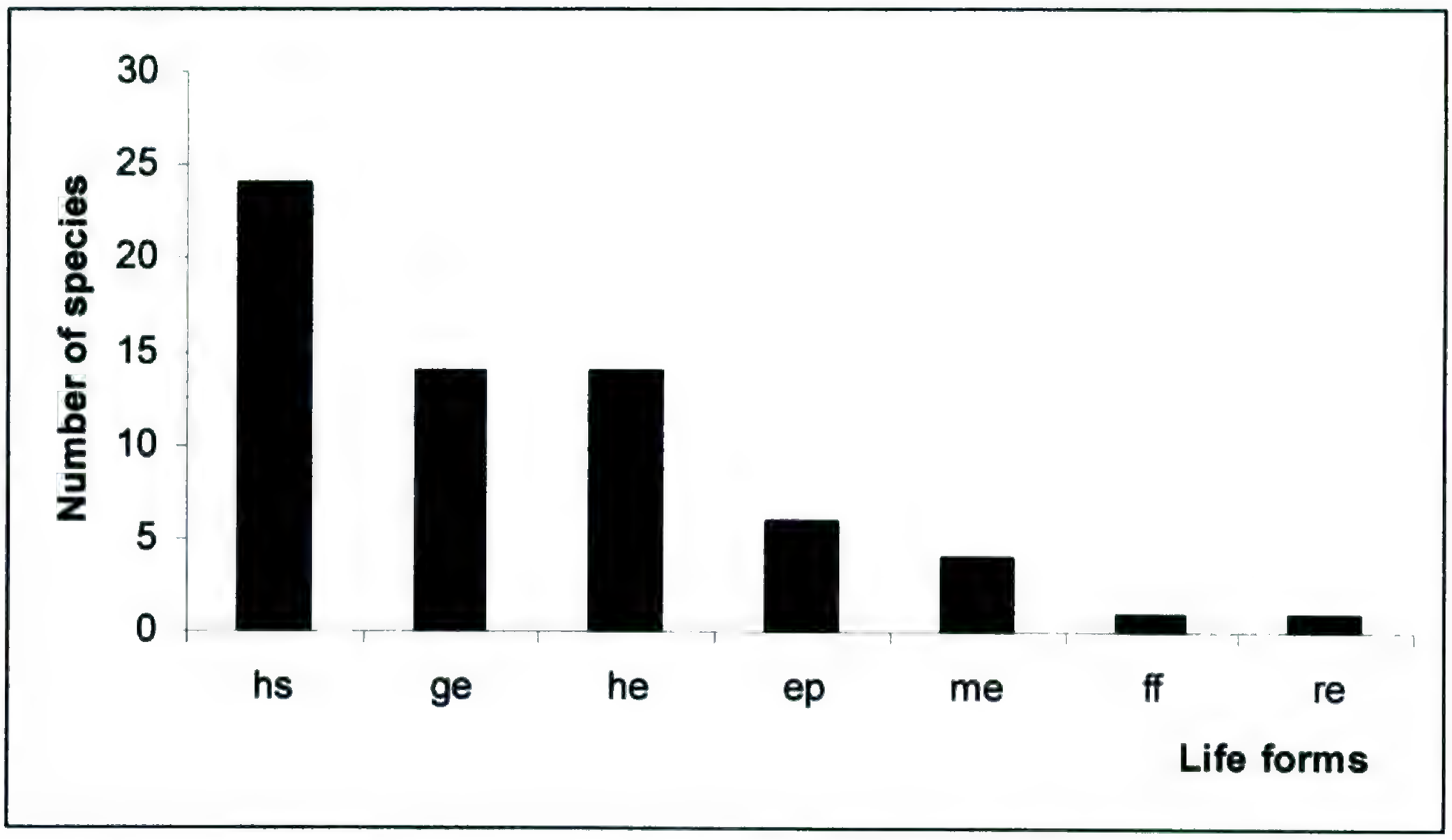

Figure 2. Life forms of aroids from the Cerrado province: hs, hemiephphytes/scandent; ge, geophytes; he, helophytes; ep, epiphytes; me, mesophytes; ff, free-floating aquatic plants; re, rheophytes.

taxa lose their aerial parts during the dry season. Meanwhile, species of *Anthurium* and *Philodendron* remain evergreen throughout the year, and sometimes they are the only plants in the outcrops that retain green leaves during the dry season.

Many species of the flora of these limestone outcrops (and also from deciduous and semideciduous mesophytic forest) follow the distribution pattern stated by Prado and Gibbs (1993), i.e., they occur mainly in three nodal areas (Caatinga, Missiones, and Piedmont) with scattered occurrence in calcareous-rich soils within the Cerrado province.

Campos rupestres. Within the Cerrado biogeographic province, two areas are usually considered as "campos rupestres": the Chapada dos Veadeiros region, in northern Goiás, and the Espinhaço range in the southeastern portion of the province, in the state of Minas Gerais. Some authors also include the Chapada dos Guimarães region in northwestern Mato Grosso. Giulietti and Pirani (1988: 43) characterized the campos rupestres of the Espinhaço Range as usually "above 900 m, in association with a high degree of outcropping and consequent reduction of soil depth." Basically the same conditions occur at the Chapada dos Veadeiros, and some components of the campo rupestre flora are common to both areas (Giulietti & Pirani, 1988). However, the aroid flora of the campos rupestres of the Espinhaço range are rich in endemic taxa (Sakuragui & Mayo, 1997; Sakuragui, 2000), whereas no species of Araceae can be considered endemic to the campos rupestres of the Chapada dos Veadeiros. In fact, if based only on the flora of Araceae, the campos rupestres of the Espinhaço range can be considered an insular micro-province within the Cerrado. Species like *Philodendron biribirense* Sakuragui & Mayo, *P. adamantinum* Schott, and *P. cipoense* Sakuragui & Mayo are only found in the Espinhaço range, and most of them are restricted to high elevations. In contrast, the most conspicuous aroid in the Chapada dos Veadeiros region is *Philodendron wullshlaegelii*, which also occurs commonly outside of the campos rupestres at lower elevations.

THE CERRADO PROVINCE WITH RESPECT TO OTHER PHYTOGEOGRAPHIC PROVINCES

The Cerrado is between two important, essentially forested provinces: the Atlantic coastal forest (Mata Atlântica) and Amazonia. In order to determine the relative importance of each one of these forested provinces in the aroid flora of the Cerrado, Jaccard's index of similarity was calculated for species and also for genera (Table 1). It is noteworthy that the species similarity between the Cerrado province and Amazonia is much higher than between Cerrado and Mata Atlântica (an index value of 0.127 vs. 0.088, respectively). However, when the similarity of genera is calculated, the situation reverses with more genera being shared between the Cerrado and Atlantic Coastal Forest (index value of 0.591) than between the Cerrado and Amazonia (index value of 0.414).

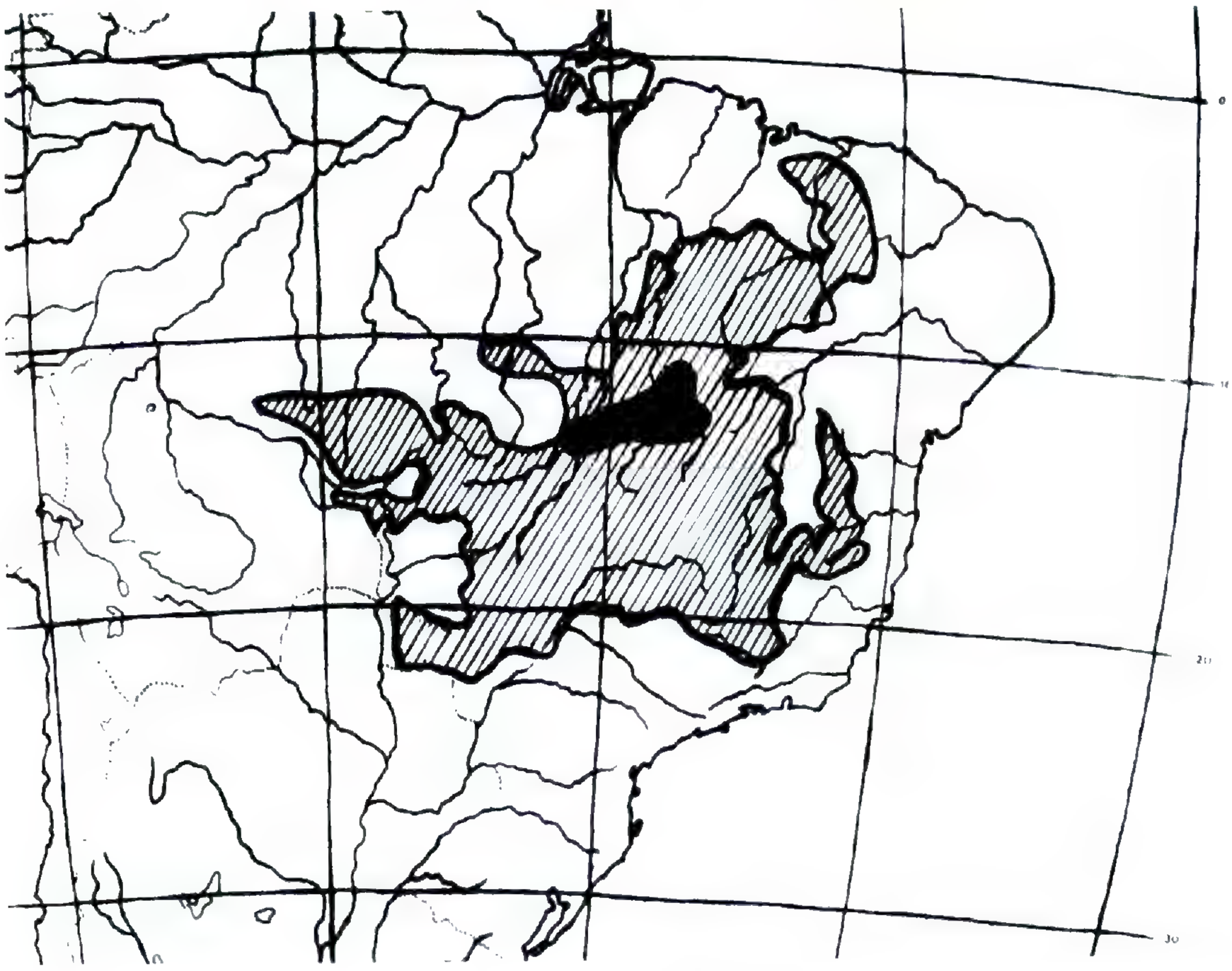

Figure 3. Known occurrence of *Gearum brasiliense* N. E. Br. (black area). Shaded area indicates the Cerrado province (see Fig. 1).

It should be emphasized that the concept of Mata Atlântica used here is broad, i.e., it also includes the subdeciduous forests of southeastern Brazil as well as those forests along the Paraná basin. Some studies have shown that these formations can be very distinct from the strictly coastal forests (Oliveira-Filho & Ratter, 1995), but the available data about the diversity of aroids do not offer such degree of resolution.

Life forms. The proportion of life forms that can be found in the Cerrado province is summarized in Figure 2. It is noteworthy that only 6 species (9.4%) are known to be true epiphytes, and this is a very low frequency when compared to other biomes in Brazil such as Mata Atlântica and Amazonia. It is also interesting to note that 14 (21.9%) of the species found are geophytes and at least 19 (29.7%) have a seasonally induced dormancy period. The proportion of helophytes is also high (21.9%), but only 4 species (6.2%) considered are true mesophytes.

Endemic taxa. Our results support that 35.9% (23 species) of the aroids found are endemic to the Cerrado phytogeographic province, namely *Anthurium megapetiolatum*, *Asterostigma cryptostylum*, *Caladium tuberosum*, *Caladium* sp. nov. [ined.], *Dieffenbachia* sp. nov. [ined.], *Dracontium* sp. nov. [ined.], *Gearum brasiliense*, *Philodendron adamantinum*, *P. biribirense*, *P. cipoense*, *P. dardanianum*, *P. flumineum*, *P. guaraense*, *P. lundii*, *P. mayoi*, *P. mello-barretoanum*, *P. rhizomatosum*, *P. uliginosum*, *P. venustifoliatum*, *Taccarum crassispathum*, *Xanthosoma plowmanii*, *X. riparium*, and *Xanthosoma* sp. nov. [ined.]. The only genus endemic to the Cerrado province seems to be *Gearum* (see its distribution in Fig. 3).

Discussion

Three separate events possibly have contributed to the actual patterns of diversity and distribution of aroids in central Brazil. They are: (1) the expansion and subsequent contraction of the rain forest during periods of less seasonality (as proposed by Prance, 1982); (2) expansion and subsequent contraction of the dry forests (as proposed by Prado & Gibbs, 1993) during periods with a more seasonal climate; and (3) filtering effect of aroid taxa from the Amazonian or Atlantic rain forest (Mata Atlântica) that enter the Cerrado province by means of riverine gallery forests, as proposed by Fernandes (1998). In this last instance, it is expected that the taxonomic diversity of these groups declines with the distance from their "source" province. Studies are ongoing in order to test this hypothesis.

Preliminary observations have shown that the Cerrado province shares more species with Amazonia than with Mata Atlântica. On the other hand, more genera are shared between the Cerrado and Mata Atlântica. The low similarity of genera be-

Table 1. Jaccard similarity index for genera and species of Araceae, between the Cerrado and the two main forested provinces in Brazil. The number of genera and species was based on Mayo et al. (1996) and Govaertz and Frodin (2002).

	Total number of species	Total number of genera	Species similarity	Genera similarity
Amazonia	184	23	0.127	0.414
Mata Atlântica	132	17	0.088	0.591

tween the Cerrado and Amazonia results from a high number of genera that are known to be endemic to the Amazonian province, such as *Alloschemone, Bognera, Ulearum, Zomicarpella* (Mayo et al., 1997), and *Anaphyllopsis* (Hay, 1988). Only the aroid genus *Dracontioides* is known to be endemic to Mata Atlântica. The level of endemism in the Araceae of the Cerrado province is not negligible. Approximately 35.9% of the species are endemic to the Cerrado; some of them have very restricted occurrence, e.g., *Philodendron guaraense* (Gonçalves, 1997). The one genus that can be considered endemic to the Cerrado is *Gearum*, which occurs in hyperseasonal savannas, flooded gallery forests, and eventually the cerradão (Bogner & Gonçalves, 1999).

The high frequency of tuberous aroids, as well as the low frequency of epiphytes, seems to demonstrate the importance of seasonality in the diversity of Araceae in central Brazil. Tuberous plants can remain leafless during the dry season.

It should be mentioned that the aroids of the Cerrado province are among the most seriously threatened in Brazil due to the fast expansion of soybean cultivation as well as pastures, which are destroying their native habitats. A more detailed knowledge of their diversity may allow the establishment of strategies to warrant their conservation as well as the maintenance of their genetic diversity.

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Appendix 1

Checklist of the Araceae occurring in the Cerrado phytogeographic province in Brazil. Asterisks (*) indicate taxa that are considered endemic to the Cerrado.

Anthurium

A. affine Schott; *A. croatii* Madison; *A. gracile* (Rudge) Schott; *A. lindmanianum* Engl.; *A. megapetiolatum* E. G. Gonç.*; *A. minarum* Sakuragui & Mayo; *A. pentaphyllum* (Aubl.) G. Don; *A. plowmanii* Croat; *A. scandens* (Aubl.) Engl.; *A. sinuatum* Benth. ex Schott; *A. solitarium* Schott

Asterostigma

A. cryptostylum Bogner*

Caladium

C. tuberosum (S. Moore) Bogner & Mayo*; *C.* sp. nov. [ined.]*

Dieffenbachia

D. aglaonematifolia; *D.* sp. nov. [ined.]*

Dracontium

D. margaretae Bogner; *D. ulei* Krause; *D.* sp. nov. [ined.]*

Gearum

G. brasiliense N. E. Br.*

Heteropsis

H. oblongifolia Kunth

Monstera

M. adansonii Schott; *M. dissecta* (Schott) N. E. Br. ex Donn. Sm.; *M. praetermissa* E. G. Gonç. & Temponi

Philodendron

P. adamantinum Engl.*; *P. biribirense* Sakuragui & Mayo*; *P. brandtianum* Krause; *P. brevispathum* Schott; *P. camposportuanum* G. M. Barroso; *P. cipoense* Sakuragui & Mayo*; *P. dardanianum* Mayo*; *P. flumineum* E. G. Gonç.*; *P. guaraense* E. G. Gonç.*; *P. guttiferum* Kunth; *P. linnaei* Kunth; *P. lundii* E. G. Gonç.*; *P. mayoi* E. G. Gonç.*; *P. megalophyllum* Schott; *P. mello-barretoanum* G. M. Barroso*; *P. minarum* Engl.; *P. rhizomatosum* Sakuragui & Mayo*; *P. solimoensense* A. C. Smith; *P. uleanum* Engl.; *P. uliginosum* Mayo*; *P. venustifoliatum* E. G. Gonç. & Mayo*; *P. wullschlaegelii* Schott; *P.* sp. nov. [ined.]

Pistia

P. stratiotes L.

Rhodospatha

R. latifolia Poepp.

Scaphispatha

S. gracilis Brongn. ex Schott

Spathicarpa

S. gardneri Schott; *S. hastifolia* Hook.

Spathiphyllum

S. gardneri Schott

Taccarum

T. crassispathum E. G. Gonç.*; *T. weddellianum* Brongn. ex Schott

Urospatha

U. sagittifolia (Rudge) Schott

Xanthosoma

X. aristeguietae (G. S. Bunting) Madison; *X. pentaphyllum* Engl.; *X. plowmanii* Bogner*; *X. riparium* E. G. Gonç.*; *X. striatipes* (Kunth) Madison; *X. syngoniifolium* Rusby; *X.* sp. nov. [ined.]*

Zomicarpa

Z. pythonium Mart. ex Schott

PROGRESS IN ORNAMENTAL AROID BREEDING RESEARCH[1]

R. J. Henny, D. J. Norman, and J. Chen[2]

ABSTRACT

Interest in development of new tropical ornamental aroid cultivars has accelerated rapidly during the past 20 years. This was stimulated by high market demand and newly published research that presented potential breeders with techniques to control aroid flowering by application of gibberellic acid sprays. In addition, research demonstrated how seed production could be enhanced by controlling relative humidity in aroid genera that were previously difficult to hybridize. Subsequent genetic studies showed foliar variegation patterns to be simply inherited, which made planning crosses easier. This paper reviews some of the important techniques used in developing new ornamental aroid cultivars.

Key words: *Aglaonema*, *Anthurium*, Araceae, aroid, *Dieffenbachia*, flowering, foliar variegation, plant breeding, seed, seed production, *Spathiphyllum*, *Syngonium*.

Ornamental aroids are a major component of the U.S. foliage plant industry and account for roughly one-third of total ornamental foliage plant sales (Fig. 1). The most important commercial ornamental aroid genera include *Aglaonema*, *Anthurium*, *Dieffenbachia*, *Epipremnum*, *Philodendron*, *Spathiphyllum*, and *Syngonium* (Henny, 1988b). All are valued for their showy foliage and ability to grow under interior conditions of relatively low light and relative humidity. The colorful and long-lasting spathes of some *Anthurium* species are highly valued as cut flowers, and the showy, white *Spathiphyllum* spathes enhance its popularity as a "flowering" foliage plant. *Syngonium* and *Epipremnum* are grown as hanging baskets or on totem poles. The other genera discussed here produce inflorescences with no ornamental value; in fact, their inflorescences are considered a nuisance by commercial producers because they decay after anthesis, remain unsightly, and must be removed before sales. Many research papers have been published regarding culture of ornamental aroids since 1970 (Conover & Poole, 1984; Joiner, 1981). Most genera require shade and prefer high humidity and warm temperatures. A basic rule of thumb is that light intensities should be low enough to preclude your hand from casting a shadow during the brightest part of the day. Light meter readings should be 1500–3500 foot candles. Winter temperatures should be 60°F minimum to prevent chilling injury or 70°F to maintain growth. Soil mixes should drain well and contain at least 50% organic matter by volume. These are only general recommendations for growing potted aroids, because some aroid genera thrive in full sun, sandy soils, and do recover from freezing.

Historically, new ornamental aroid cultivars originated either from mutations of established cultivars or from introduction of new plants collected in the wild (Wilfret & Sheehan, 1981). During the past 20 years, however, plant breeding has had an expanding role in the introduction of new cultivars. Different aroid genera that are currently being bred at the Mid-Florida Research and Education Center–Apopka, including their important horticultural traits and named hybrids released, are listed in Table 1. Increased knowledge of aroid breeding methods and the development of plant tissue culture for fast, reliable propagation have stimulated new aroid cultivar development. Both of these factors were fostered in part by their market's high crop value and its demand for new cultivars. Using tissue culture, a new aroid cultivar can be propagated rapidly to commercial production levels within one to two years instead of five to seven years required utilizing standard cutting or division techniques.

[1] Successful breeding of new plants of any plant genus requires a source of diverse germplasm. We are fortunate that many excellent botanical gardens and personal collections exist, and that their plant materials have been generously made available for our research purposes. We indeed owe much to many dedicated botanists, horticulturists, and avid plant people who work tirelessly collecting and cataloging data on new sources of aroids. Without their continued efforts, the development of new ornamental aroid cultivars would be severely limited. We extend a heartfelt thanks to all of them.

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Figure 1. Different aroid hybrids used in the Mid-Florida Research and Education Center foliage breeding program (clockwise from bottom right), *Anthurium*, *Dieffenbachia*, *Aglaonema*, *Spathiphyllum*, and *Aglaonema*.

Flower Structure and Flowering Cycles

Aroid inflorescences consist of a spadix enclosed by a spathe. The spadix is a fleshy spike covered with many small unisexual or bisexual flowers, depending on the genus. *Aglaonema*, *Dieffenbachia*, *Philodendron*, and *Syngonium* display unisexual flowers; they contain male flowers on the upper half and female flowers on the lower portion of the spadix, with a small area between that may be devoid of flowers. *Anthurium*, *Epipremnum*, and *Spathiphyllum* have bisexual flowers. In these, the entire spadix is covered with complete florets.

For breeding, flower production is vital. The ideal situation exists in mature *Anthurium*, where flower production is continuous throughout the year for many species. Differences in the natural flowering cycles of some aroid species within the same genus can be frustrating for plant breeders. Careful planning is required to ensure a sufficient supply of flowers for breeding, especially in genera such as *Aglaonema* and *Dieffenbachia*, which only produce three to five inflorescences per stem per year. Natural flowering of *Aglaonema*, *Dieffenbachia*, *Philodendron*, and *Spathiphyllum* occurs in late winter or spring in heated greenhouses in Florida (flowering times vary depending on environmental conditions, species, and cultivars). For example, in a greenhouse heated to a minimum night temperature of 50°F, plants of the same species or cultivar will flower approximately one month later than in a comparable greenhouse heated to 60°F.

Chemical Induction of Flowering

At the Mid-Florida Research and Education Center in Apopka, our aroid breeding program has benefited from studies that revealed that *Dieffenbachia* (Henny, 1980a), *Spathiphyllum* (Henny, 1981), *Syngonium* (Henny et al., 1999), and *Aglaonema* (Henny 1983b) can be induced to flower throughout the year if plants are treated with gibberellic acid (GA_3), a plant hormone. Treatment generally consists of a single foliar spray of 250 ppm GA_3 from a commercially available GA_3 source (GibGro, 4% gibberellic acid, Agtrol Chemical Products, Houston, Texas 77074) and mixed at 1 ounce per gallon of water. Following treatment, plants will flower in three to five months, depending on the genus. Fortunately, different species and cultivars within a genus generally flower together following GA_3 treatment. An additional benefit of using GA_3 to induce flowering is that treated plants produce more flowers than those not treated. Some

Figure 2. *Dieffenbachia* inflorescences (left to right) in the bud stage; day of anthesis with spathe unfurled and receptive for pollination; with pollen produced two days after anthesis; and with spathe partially removed to show basal female flowers.

Figure 3. A close-up (30×) of individual male flowers on a single *Dieffenbachia* inflorescence showing pollen being dehisced.

inflorescences produced via GA_3 treatment may be deformed, but no detrimental effects on fertility as measured by pollen production or seed set have been observed.

Pollination Techniques and Pollen Germination

Anthesis in *Aglaonema* and *Dieffenbachia* is indicated by the unfurling of the upper spadix to expose the male flowers, a time when female flowers are receptive (Fig. 2). However, pollen on the same inflorescence is not dehisced until two days later (Fig. 3). It is therefore necessary to obtain pollen from another inflorescence and manually transfer it to the seed parent. This can be done by brushing pollen into a small container. If desired, the entire inflorescence may be removed and situated so the spathe catches pollen that becomes dislodged from the spadix. Pollination can be easily accomplished utilizing the brush employed to collect the pollen. It is helpful to make the brush somewhat sticky by touching the stigmatic surfaces of female flowers before dipping it into the pollen supply for transfer to the stigmatic surfaces of receptive flowers (Fig. 4).

Pollen germination studies with *Aglaonema* revealed that although seed was obtained from flowers that were pollinated one day after spathe unfurling, the number of seeds was reduced (Henny, 1988a). Receptivities of *Aglaonema* and *Dieffenbachia* flowers last at least 24 hours. Female flowers' stigmatic surfaces do not support pollen germination once pollen is produced by male flowers within the same inflorescence (Henny, unpublished). By this time, stigmatic surfaces have become discolored and soft.

Immediately following pollination, *Dieffenbachia* flowers require 100% relative humidity to ensure pollen germination (Henny, 1980b). This can be done by wrapping the entire spadix with moistened paper toweling within a plastic bag (Fig. 5). The bag should be removed the next morning so it does not interfere with pollen production. Maximum pollen germination (Fig. 6) and seed yield (Fig. 7) in *Aglaonema* also requires high relative humidity after pollination (Henny, 1985).

In genera with bisexual flowers (e.g., *Anthurium* and *Spathiphyllum*) the spathe unfurls and exposes the spadix several days before female flowers are receptive. Male and female *Spathiphyllum* flowers

Figure 4. Pollination of a *Dieffenbachia* inflorescence using a soft brush.

Table 1. A listing of the five aroid genera, major species used in breeding, important horticultural traits to select for in each genus, and a summary of the hybrid cultivars released by Mid-Florida Research and Education Center, Apopka, Florida.

Genus	Important species used in breeding	Important traits to select for in hybrids	Hybrid cultivars released by MREC
Aglaonema	*nitidum* (Jack) Kunth	leaf shape and variegation pattern	Stripes
	commutatum Schott	petiole color	Flamingo
	costatum N. E. Br.	branching and vigor	Silver Bay
	rotundum N. E. Br.	chilling resistance	Golden Bay
Anthurium	*andraeanum* Linden	early flowering	Southern Blush
	amnicola Dressler	flower color and size	Red Hot
	antioquense Engl.	branching and vigor	Show Biz
	crystallinum Linden & Andre	disease resistance	
	scherzeranum Schott	compact growth habit	
Dieffenbachia	*imperialis* Linden & Andre	leaf shape and color	Triumph; Victory
	leopoldii W. Bull	petiole color	Tropic Star; Sparkles
	maculata (Lodd.) D. Don	branching and vigor	Star White; Star Bright
	oerstedtii Schott	disease and chilling resistance	Starry Nights
Spathiphyllum	*cannifolium* (Dryland) Schott	early flowering	none*
	floribundum (Linden & Andre) N. E. Br.	continual flowering	
	patinii (Hogg) N. E. Br.	disease resistance	
	wallisii Regil	male sterility	
Syngonium	*auritum* (L.) Schott	leaf color and size	none**
	podophyllum Schott	branching	
	wendlandii Schott	dwarf size	
		disease resistance	

* Several hybrids released in 1998–1999 for propagation and trial growing.
** New program initiated during 1999.

Figure 5. A *Dieffenbachia* inflorescence wrapped in wet paper toweling and enclosed in a plastic bag for one day immediately after pollination to ensure pollen germination.

mature over a two- to three-day period. In *Anthurium*, female flowers at the base of the spadix mature first and gradually over a two-week period, additional florets become receptive toward the top of the spadix (Kamemoto et al., 1968). In these genera, receptivity is indicated by a glistening shine of stigmatic surfaces.

Once no longer receptive, stigmatic surfaces dry and turn brown. At this stage pollen appears along the spadix's base, proceeding toward the top. Because of the uneven maturation of individual male flowers, *Anthurium* pollen is available for up to two weeks, while *Spathiphyllum* pollen can be harvested for two to three days. *Anthurium* pollen can be transferred by collecting it on your finger tips then gently rubbing it on receptive stigmas. *Spathiphyllum* pollen is readily collected by gently tapping the inflorescence and collecting the pollen as it falls into a container held underneath. Subsequent pollinations are made using a soft brush.

To achieve maximum seed production, an *Anthurium* spadix may need to be pollinated more than once because, as discussed above, female flowers mature sequentially from the bottom to the top of the spadix over a two-week period. However, it is possible to fertilize an entire *Spathiphyllum* spadix with one pollination if you wait until all the styles appear receptive, which may require two to three days. Following pollination, no environmental manipulation regarding increasing relative humidity, as is required with *Aglaonema* and *Dieffenbachia*, is needed to ensure *Anthurium* or *Spathiphyllum* seed set.

Very little information is available on aroid pollen storage. Pollen in short supply can be stored in a container in a refrigerator and a high humidity environment. Enclose the container with, but not in contact with, a wet paper towel or some other moistened material. *Philodendron* and *Spathiphyllum* pollen may be stored in this manner for several days to weeks. *Aglaonema* and *Dieffenbachia* pollen germination declines within one to two days of storage, so it is best to use fresh pollen for them.

Seed Development and Germination

Dieffenbachia fruits mature in five to six months (Fig. 8), *Anthurium* fruits require six months, and *Aglaonema* fruits mature in four to six months, although some hybrids have taken up to one year. In *Dieffenbachia* and *Aglaonema*, seed maturity is indicated by a red seed covering. *Anthurium* and *Spathiphyllum* spadices begin to change color, soften, and seeds become visible.

To enhance germination, seeds are separated from the spadix to lessen the chance of disease contamination from the decaying fruit. For *Dieffenbachia* and *Aglaonema*, which have large seeds, the fleshy seed covering is removed from picked, red, berry-like fruit before planting the seed. Genera with large numbers of small seeds such as *Spathiphyllum* are more difficult. The entire spadix is placed in a plastic bag with a little water. The spadix decays in a few days, allowing the seeds to be removed by gently washing them on a screen small enough to allow only the rotted spadix tissue through. Cleaned seeds should be planted before they dry.

High germination is achieved if seeds are sown on top of a moist medium containing up to 50% peat moss by volume and covered with plastic to prevent drying. Aroid seeds begin to grow as soon as sown. The medium should be kept at a minimum of 70°F. Seedlings are repotted after the first true leaves are produced. Most aroid seedlings require one year of growth before they are evaluated.

Inheritance of Foliar Variegation

Foliar variegation in *Dieffenbachia* and *Aglaonema* is dominant over non-variegation (i.e., green

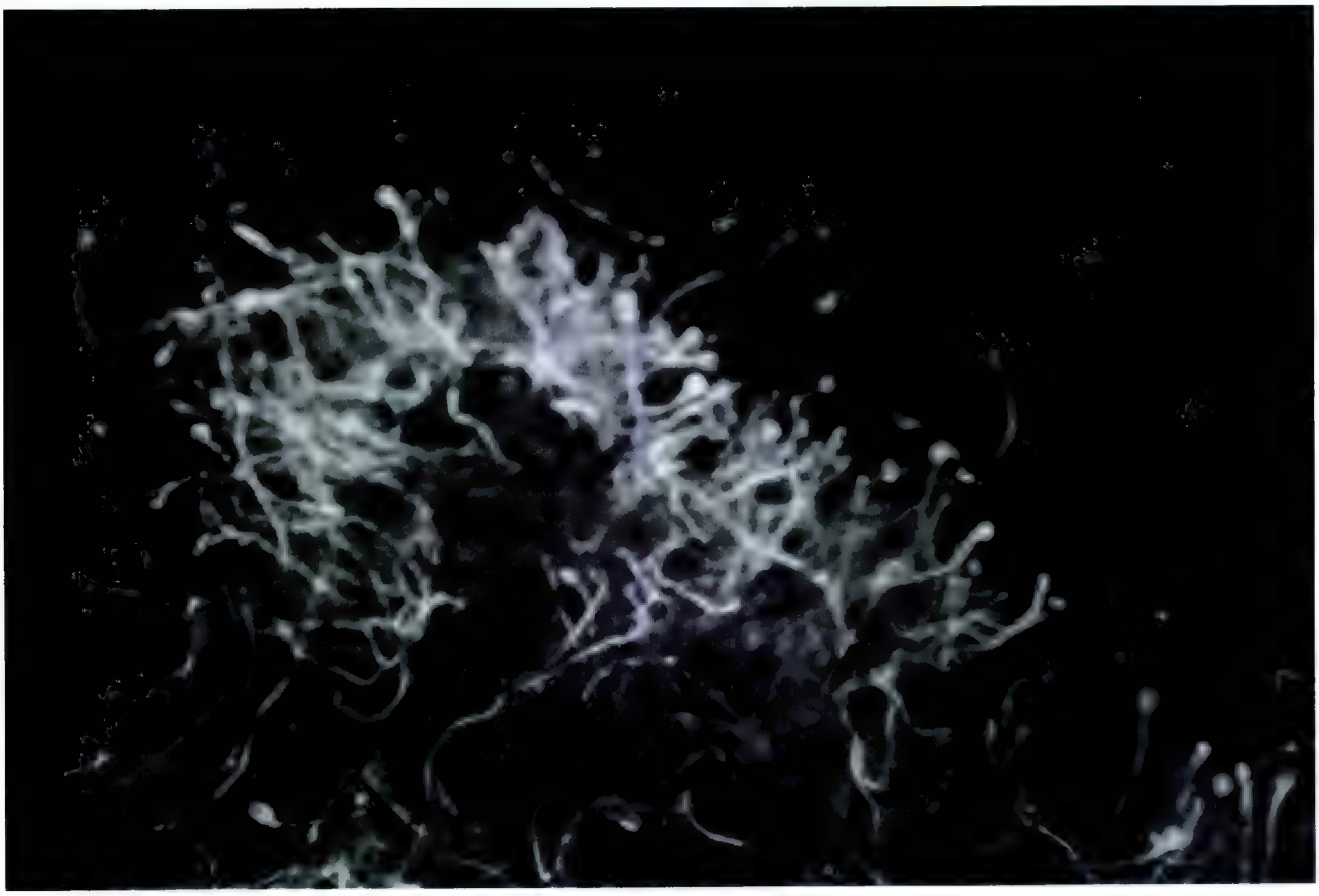

Figure 6. A single *Aglaonema* flower pollinated at high (100%) relative humidity. Many pollen tubes are evident on the stigmatic surface.

Figure 7. Several developing *Aglaonema* fruit at four months after pollination. Each fruit contains a single seed. The fruit turn red when mature.

Figure 8. Three *Dieffenbachia* inflorescences with mature fruit that have been harvested for cleaning and planting.

Figure 9. Foliar variegation patterns (left to right) of *Dieffenbachia maculata* 'Perfection,' *D. m.* 'Camille,' and a hybrid containing the alleles for both patterns. The 'Camille' pattern masks the 'Perfection' pattern except near the outer leaf edges.

Figure 10. Foliar variegation patterns (left to right) of *Aglaonema nitidum* 'Ernesto's Favorite,' *A. n.* 'Curtisii,' and their hybrid (right), which expresses a combination of both parental foliar variegation patterns.

leaves). A single dominant allele (*Pv*) determines the presence of a variegation pattern typical for *A. maculata* 'Perfection' (Henny, 1982). Studies showed that mutation of the *Pv* allele to *Pv'* produced the variegation pattern present in *D. maculata* 'Camille' (Henny, 1986b). The *Pv'* allele masks the expression of the *Pv* allele (Fig. 9). Inheritance of a white foliar midrib in *Dieffenbachia* is also controlled by a single dominant gene linked to the gene controlling foliar variegation (Henny, 1983a). The dominant alleles for each trait are carried on opposite, homologous chromosomes.

Inheritance of foliar variegation in *Aglaonema* is similar to *Dieffenbachia*. Six foliar variegation patterns of *Aglaonema* have been reported to be governed by a single locus, multiple allelic system, wherein each distinct pattern is controlled by a separate dominant allele (Henny, 1986a). All six alleles studied were codominant; therefore, a maximum of two variegation patterns in the same plant could be expressed (Fig. 10). Plants that were heterozygous for variegation would express only one pattern while homozygous recessive plants would be nonvariegated. The combination of two different variegation patterns in a single hybrid has allowed creation of plants with novel patterns (Henny, 1986a). Additional variegation patterns in *Aglaonema* are currently being studied and appear to be inherited in the same manner.

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A PRELIMINARY SURVEY OF PETIOLAR COLLENCHYMA IN THE ARACEAE[1]

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ABSTRACT

This article presents a preliminary systematic survey of 115 species from 56 genera (approximately 51% of the genera) of Araceae in which the pattern of petiolar collenchyma (or its absence) is described and classified. This feature appears very conservative within the genera, apparently not changing qualitatively with developmental or environmental conditions. Cross sections at the midpoint between petiole base and apex were mainly studied, but apical and basal sections were also observed in those genera where the collenchyma is absent at petiole midpoint. Three patterns are defined: (1) collenchyma absent at the midpoint between petiole base and apex; (2) a peripheral continuous or interrupted ring of collenchyma (philodendroid pattern); (3) rounded strands of collenchyma concentrically disposed and associated with peripheral vascular bundles (colocasioid pattern). No genera with bisexual flowers so far analyzed have collenchyma at petiole midpoints, although this usually occurs at apex and base. Monoecious genera can display all three patterns, but pattern 1 appears restricted to tribe Zamioculcadeae and the genus *Anubias*. The presence of a fully collenchymatous petiole seems to appear only in more derived genera in the Araceae: it may be an apomorphic feature within the family.

Key words: Araceae, collenchyma, petiole, pulvinus, sclerenchyma.

Anatomical features are, in many cases, reasonably important for the taxonomic definition of some groups and are considered to be as valuable as morphological ones (Stace, 1980). In taxa in which gross morphological features are non-informative, studies of comparative plant anatomy are very useful.

The anatomy of the Araceae has been studied mainly by French (1997). His studies have been important in helping to define the supra-generic classification of the family (Mayo et al., 1997). Despite the broad range of these studies (across taxa and across organs and tissues), little attention has been directed to leaves and petioles.

Although restricted in its occurrence in the monocotyledons (Fahn, 1990), collenchyma is found in various genera of the Araceae. It is common in growing aerial organs as supporting tissue, being characterized by the presence of thick-walled cells with non-lignified primary walls. Collenchyma is also noted for its plasticity, i.e., this tissue retains its capacity to be deformed, although its function is related to mechanical support.

Probably the first to observe patterns of support tissue in petioles of Araceae was Engler (1920), and he published most of the current knowledge about this topic. Engler considered the patterns of collenchyma taxonomically meaningless because they were not congruent with his classification. Later Solereder and Meyer (1928) described the petiole anatomy in various species, observing a fused ring of collenchyma in *Asterostigma, Dieffenbachia, Homalomena, Philodendron, Schismatoglottis,* and *Spathantheum.* They also observed that *Peltandra, Typhonodorum,* many genera of the tribes Caladieae and Colocasiae, and most Old World Areae had collenchymatous sheaths associated with the vascular bundles.

In a short communication on the determination of collenchyma patterns in the Araceae, Gonçalves and Paiva (1995) described two basic patterns of distribution of this tissue in petioles. They were named "colocasioid" and "philodendroid," based on the Englerian subfamilies in which each pattern was first observed. The former was characterized by the presence of rounded strands of collenchyma concentrically disposed and the latter by a ring of collenchyma surrounding the whole petiole that could be either continuous or interrupted.

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Given the potential significance of such a feature for phylogenetic studies in aroids, we present here a preliminary survey of petiolar patterns of collenchyma in the Araceae.

Materials and Methods

Plants from 56 genera were surveyed, covering approximately 51% of the currently accepted genera for the family (109). This number of genera in the family was calculated using the previously accepted number of 106 (Mayo et al., 1997) minus *Lazarum* (Hay, 1997) minus *Sauromatum* (Hetterscheid & Boyce, 2000) (both merged with *Typhonium*) plus the five genera of "lemnoids" (French et al., 1995; Les & Crawford, 1999). We analyzed 115 species (Table 1), all from fresh material. When possible, more than one species for each genus was sampled in order to observe the infrageneric variation of collenchyma patterns. Wild-collected plants or aroids of cultivated origin were used (vouchers are deposited in the herbarium of the University of Brasília). Since many non-Brazilian genera were sampled from cultivated material (usually from unknown origin), we also vouchered all of them. All plants were identified and surveyed for the pattern of supporting tissues in the petioles.

To determine the pattern of collenchyma, fully expanded foliage leaves were collected. Transverse sections at the midpoint between petiole base and apex were studied, except in *Pistia stratiotes*, in which the base of the sessile leaf was used. Material not collected near the laboratory (e.g., from wild populations) was preserved in 50% glycerin solution to keep it hydrated and preserve the collenchyma. In some genera with bisexual flowers, sections were also made at the base and/or apex of the petiole, particularly when a pulvinus was present.

Transverse sections were made by hand from each petiole. The sections obtained were submitted to a vacuum to remove air bubbles from the tissue. The sections were then stained using Astra Blue and Fuchsin counter stains or subjected to histochemical tests for pectins (Ruthenium Red) and lignins (acid phloroglucin) (Johansen, 1940). The sections were then mounted in semi-permanent preparations with aqueous glycerin.

The collenchyma patterns were recorded by light photomicrography and drawn using a drawing attachment model Olympus BH2. A complete list with all material surveyed is presented in Table 1.

Results

For our preliminary observations, it was noted that the pattern of distribution of collenchyma in the petioles of the Araceae does not change qualitatively with the age of the plants. As far as our analysis showed, all species from the same genus presented the same patterning, which suggested that variation in the pattern of collenchyma between taxa could be taxonomically useful. It was also observed that there was no significant change in relation to growing conditions.

The collenchyma patterns observed of all surveyed taxa are shown in Table 1. Three patterns were identified (see Fig. 1): (1) collenchyma absent, at least from the midpoint of the petiole (Fig. 2A) presenting sclerenchyma as the main supporting tissue; (2) a peripheral ring of collenchyma (philodendroid pattern) (Fig. 2C), which can be either continuous or interrupted; (3) rounded strands of collenchyma concentrically disposed (colocasioid pattern) (Fig. 2D). All taxa studied could be referred to one of these patterns, as follows:

Subfamily Pothoideae

The representative genus considered was *Anthurium* with the nine observed species showing no collenchyma at the midpoint between petiole base and apex. The vascular bundles are accompanied by sclerenchyma and some species (e.g., *A. acutum* and *A. longifolium*) have the outermost vascular bundles united by a continuous sheath of sclerenchyma.

Subfamily Monsteroideae

The taxa studied here include *Heteropsis* (1 species), *Rhaphidophora* (1), *Epipremnum* (1), *Scindapsus* (1), *Spathiphyllum* (5), *Stenospermation* (2), *Monstera* (2), and *Rhodospatha* (2). All surveyed genera lacked collenchyma at the midpoint between petiole base and apex.

Subfamily Lasioideae

The genera surveyed were *Cyrtosperma* (1 species), *Dracontium* (2), *Dracontioides* (1), *Lasia* (1), *Pycnospatha* (1), and *Urospatha* (1). None of the genera have collenchyma at the midpoint between petiole base and apex.

Subfamily Aroideae

With the exception of *Zamioculcas*, *Gonatopus*, *Anubias*, and *Ambrosina*, where collenchyma is absent from petiole mid regions, all genera from this subfamily present true collenchyma as the main supportive tissue in the petioles. The collenchyma may be isolated from the epidermis by a few layers of parenchyma (e.g., *Aglaonema crispum* and *Dief-*

Table 1. Genera and species of the Araceae studied for the pattern of collenchyma in the petiole. Subfamilies and tribes are ordered as they appear in Mayo et al. (1997).

Taxa	Source	Collenchyma pattern at the midpoint between base and apex of the petiole
SUBFAMILY POTHOIDEAE		
Tribe Anthurieae		
Anthurium		
A. acutum N. E. Br.	Brazil. Santa Catarina: *Gonçalves 321* (UB)	collenchyma absent
A. longifolium (Hoffmans.) G. Don	Brazil. Espirito Santo: *Gonçalves 568* (UB)	collenchyma absent
A. mourai Engl.	Brazil. Minas Gerais: *Gonçalves 724* (UB)	collenchyma absent
A. obtusum (Engl.) Grayum	Brazil. Amapá: *Gonçalves 514* (UB)	collenchyma absent
A. plowmanii Croat	Brazil. Mato Grosso do Sul: *Gonçalves 193* (UB)	collenchyma absent
A. rubrinervium G. Don	Brazil. Amapá: *Gonçalves 540* (UB)	collenchyma absent
A. scandens (Aubl.) Engl.	Brazil. Rio Grande do Sul: *Gonçalves 606* (UB)	collenchyma absent
A. sinuatum Benth. ex Schott	Brazil. Goiás: *Gonçalves 355* (UB)	collenchyma absent
A. solitarium Schott	Brazil. Espírito Santo: *Gonçalves 571* (UB)	collenchyma absent
SUBFAMILY MONSTEROIDEAE		
Tribe Spathiphylleae		
Spathiphyllum		
S. cannifolium (Dryand.) Schott	Brazil. Cultivated at Belo Horizonte Botanical Garden, *Gonçalves 746* (UB)	collenchyma absent
S. floribundum N. E. Br.	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 748* (UB)	collenchyma absent
S. gardneri Schott	Brazil. Goiás: *Gonçalves 82* (UB)	collenchyma absent
S. humboldtii Schott	Brazil. Amapá: *Gonçalves 478* (UB)	collenchyma absent
S. wallisii Regel	Brazil. Cultivated at Belo Horizonte Botanical Garden, *Gonçalves 747* (UB)	collenchyma absent
Tribe Heteropsideae		
Heteropsis		
H. oblongifolia Kunth	Brazil. Bahia: *Gonçalves 134* (UB)	collenchyma absent
Monstera		
M. adansonii Schott	Brazil. Bahia: *Gonçalves 417* (UB0	collenchyma absent
M. deliciosa Liebm.	Brazil. Cultivated at University of Brasília, *Gonçalves 753* (UB)	collenchyma absent
Rhaphidophora		
R. decursiva (Roxb.) Schott	Brazil. Cultivated at University of São Paulo, *Gonçalves 760* (UB)	collenchyma absent
Epipremnum		
E. pinnatum (L.) Engl.	Brazil. Cultivated at University of São Paulo, *Gonçalves 759* (UB)	collenchyma absent
Rhodospatha		
R. latifolia Poepp.	Brazil. Bahia: *Gonçalves 133* (UB)	collenchyma absent
R. oblongata Poepp. & Endl.	Brazil. Amapá: *Gonçalves 505* (UB)	collenchyma absent
Scindapsus		
S. pictus Hassk.	Brazil. Cultivated at Belo Horizonte Botanical Garden. *Gonçalves 755* (UB)	collenchyma absent

Table 1. Continued.

Taxa	Source	Collenchyma pattern at the midpoint between base and apex of the petiole
Stenospermation		
S. angustifolium Hemsl.	Panama. Panamá: *Sucre 4733* (RB)	collenchyma absent
S. multiovulatum (Engl.) N. E. Br.	Brazil. Amapá: *Gonçalves 548* (UB)	collenchyma absent
SUBFAMILY LASIOIDEAE		
Cyrtosperma		
C. merkusii Schott	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 620* (UB)	collenchyma absent
Dracontioides		
D. desciscens (Schott) Engl.	Brazil. Bahia: *Gonçalves 409* (UB)	collenchyma absent
Dracontium		
"D. bogneri" G. H. Zhu, ined.	Brazil. Tocantins: *Gonçalves 279* (UB)	collenchyma absent
D. margaretae Bogner	Brazil. Tocantins: *Gonçalves 97* (UB)	collenchyma absent
Lasia		
L. spinosa (L.) Thwaites	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 619* (UB)	collenchyma absent
Pycnospatha		
P. arietina Thorel & Gagnep.	Brazil. Cultivated in Belo Horizonte Botanical Garden, obtained from John Banta (U.S.A.). *Gonçalves 754* (UB)	collenchyma absent
Urospatha		
U. sagittifolia (Rudge) Schott	Brazil. Tocantins: *Gonçalves 99* (UB)	collenchyma absent
SUBFAMILY AROIDEAE		
Tribe Zamioculcadeae		
Gonatopus		
G. boivinii (Decne.) Engl.	Brazil. Cultivated at Belo Horizonte Botanical Garden, sent by Josef Bogner to Victor Soukoup and forwarded to Brazil, *Gonçalves 761* (UB)	collenchyma absent
Zamioculcas		
Z. zamiifolia (Lodd.) Engl.	Brazil. Cultivated at Belo Horizonte Botanical Garden, sent by Paul Resslar (U.S.A.), *Gonçalves 758* (UB)	collenchyma absent
Tribe Dieffenbachieae		
Dieffenbachia		
D. elegans Jonker & A. M. E. Jonker	Brazil. Amapá: *Gonçalves 503* (UB)	philodendroid
D. paludicola N. E. Br.	Brazil. Amapá: *Gonçalves 476* (UB)	philodendroid
D. seguine (Jacq.) Schott	Brazil. Rondônia: *Gonçalves 112* (UB)	philodendroid
Tribe Spathicarpeae		
Asterostigma		
A. cryptostylum Bogner	Brazil. Distrito Federal: *Gonçalves 71* (UB)	philodendroid
A. lombardii E. G. Gonç.	Brazil. Minas Gerais: *Lombardi 658* (BHCB)	philodendroid
A. riedelianum Schott	Brazil. Bahia: *Gonçalves 418* (UB)	philodendroid

Table 1. Continued.

Taxa	Source	Collenchyma pattern at the midpoint between base and apex of the petiole
Gearum		
G. brasiliense N. E. Br.	Brazil. Tocantins: *Gonçalves 109* (UB)	philodendroid
Gorgonidium		
G. vermicidum (Speg.) Bogner & Nicolson	Argentina. Tucumán: *Hennipman 4047* (L)	philodendroid
Mangonia		
M. tweedieana Schott	Brazil. Rio Grande do Sul: *Gonçalves 611* (UB)	philodendroid
Spathantheum		
S. intermedium Bogner	Peru. Cuzco: *Munn 148* (L)	philodendroid
Spathicarpa		
S. gardneri Schott	Brazil. Distrito Federal: *Gonçalves 72* (UB)	philodendroid
S. hastifolia Hook.	Brazil. Santa Catarina: *Gonçalves 457* (UB)	philodendroid
S. lanceolata Engl.	Brazil. Rio Grande do Sul: 612 (UB)	philodendroid
Synandrospadix		
S. vermitoxicus (Griseb.) Engl.	Bolivia. Sucre: *Zecher s.n.* (M)	philodendroid
Taccarum		
T. crassispathum E. G. Gonç.	Brazil. Goiás: *Gonçalves 104* (UB)	philodendroid
T. weddellianum Brongn. ex Schott	Brazil. Mato Grosso do Sul: *Gonçalves 198* (UB)	philodendroid
Tribe Philodendreae		
Philodendron		
P. camposportoanum G. M. Barroso	Brazil. Goiás: *Gonçalves 43* (UB)	philodendroid
P. bipinnatifidum Schott ex Endl.	Brazil. Distrito Federal: *Gonçalves 66* (UB)	philodendroid
P. cipoense Sakuragui & Mayo	Brazil. Minas Gerais: *Gonçalves 339* (UB)	philodendroid
P. linnaei Kunth	Brazil. Rio de Janeiro: *Gonçalves 278* (UB)	philodendroid
P. flumineum E. G. Gonç.	Brazil. Distrito Federal: *Gonçalves 50* (UB)	philodendroid
P. fragrantissimum (Hook.) G. Don	Brazil. Bahia: *Gonçalves 139* (UB)	philodendroid
P. insigne Schott	Brazil. Bahia: *Gonçalves 138* (UB)	philodendroid
P. pedatum (Hook.) Kunth	Brazil. Bahia: *Gonçalves 402* (UB)	philodendroid
P. hederaeum (Jacq.) Schott	Brazil. Espírito Santo: *Gonçalves 583* (UB)	philodendroid
P. squamiferum Poepp.	Brazil. Amapá: *Gonçalves 504* (UB)	philodendroid
P. uliginosum Mayo	Brazil. Distrito Federal: *Gonçalves 60* (UB)	philodendroid
Tribe Homalomeneae		
Homalomena		
H. wallisii Regel	Brazil. Cultivated at Belo Horizonte Botanical Garden, *Gonçalves 756* (UB)	philodendroid
H. wendlandii Schott	Brazil. Rondônia: *Gonçalves 212* (UB)	philodendroid

Table 1. Continued.

Taxa	Source	Collenchyma pattern at the midpoint between base and apex of the petiole
Tribe Anubiadeae		
Anubias		
A. afzelii Schott	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 621* (UB)	collenchyma absent
A. hastifolia Engl.	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 618* (UB)	collenchyma absent
Tribe Schismatoglottideae		
Schismatoglottis		
S. acutangula Engl.	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 617* (UB)	philodendroid
S. neoguineensis (André) N. E. Br.	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 762* (UB)	philodendroid
		philodendroid
Tribe Cryptocoryneae		
Cryptocoryne		
C. cordata Griff.	Brazil. Cultivated at Brasília, *Gonçalves 757* (UB)	colocasioid
Tribe Zomicarpeae		
Zomicarpa		
Z. riedeliana Schott	Brazil. Maranhão: *Gonçalves 157* (UB)	colocasioid
Tribe Caladieae		
Caladium		
C. bicolor (Aiton) Vent.	Brazil. Goiás: *Gonçalves 81* (UB)	colocasioid
C. humboldtii Schott	Brazil. Cultivated at São Paulo, *Gonçalves 745* (UB)	colocasioid
Scaphispatha		
S. gracilis Brongn. ex Schott	Brazil. Maranhão: *Gonçalves 147* (UB)	colocasioid
Syngonium		
S. angustatum Schott	Brazil. Cultivated at São Paulo: *Gonçalves 743* (UB)	colocasioid
S. auritum Schott	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 764* (UB)	colocasioid
S. vellozianum Schott	Brazil. Bahia: *Gonçalves 136* (UB)	colocasioid
Xanthosoma		
X. aristeguietae (G. S. Bunting) Madison	Brazil. Mato Grosso do Sul: *Gonçalves 202* (UB)	colocasioid
X. helleborifolium (Jacq.) Schott	Brazil. Goiás: *Gonçalves 91* (UB)	colocasioid
X. maximilianii Schott	Brazil. Bahia: *Gonçalves 135* (UB)	colocasioid
X. pentaphyllum (Vell.) Engl.	Brazil. Distrito Federal: *Gonçalves 30* (UB)	colocasioid
X. plowmanii Bogner	Brazil. Tocantins: *Gonçalves 143* (UB)	colocasioid
X. riedelianum Schott	Brazil. Cultivated at Belo Horizonte Botanical Garden, *Gonçalves 763* (UB)	colocasioid
X. sagittifolium (L.) Schott	Brazil. Cultivated at Rondônia, *Gonçalves 238* (UB)	colocasioid
X. striatipes (Kunth) Madison	Brazil. Distrito Federal: *Gonçalves 67* (UB)	colocasioid
X. acutum E. G. Gonç.	Brazil. Amapá: *Gonçalves 556* (UB)	colocasioid

Table 1. Continued.

Taxa	Source	Collenchyma pattern at the midpoint between base and apex of the petiole
Tribe Nephthytideae		
Anchomanes		
A. difformis (Blume) Engl.	Brazil. Cultivated at Belo Horizonte Botanical Garden, sent by Robert McClure (Australia), *Gonçalves 738* (UB)	philodendroid
Nephthytis		
N. poissonii (Engl.) N. E. Br.	Brazil. Cultivated at Belo Horizonte Botanical Garden, sent by Josef Bogner to Victor Soukoup (U.S.A.) and forward to Brazil, *Gonçalves 737* (UB)	philodendroid
Tribe Aglaonemateae		
Aglaonema		
A. commutatum Schott	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 735* (UB)	philodendroid*
A. costatum N. E. Br.	Brazil. Cultivated in São Paulo, *Gonçalves 765* (UB)	philodendroid*
A. crispum (Pitcher & Manda) Nicolson	Brazil. Cultivated at Belo Horizonte Botanical Garden, *Gonçalves 766* (UB)	philodendroid*
A. modestum Engl.	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 767* (UB)	philodendroid*
Tribe Culcasieae		
Cercestis		
C. mirabilis (N. E. Br.) Bogner	Brazil. Cultivated at Burle-Marx's collection at Rio de Janeiro, *Gonçalves 616* (UB)	philodendroid
Tribe Montrichardieae		
Montrichardia		
M. linifera (Arruda) Schott	Brazil. Bahia: *Gonçalves 140* (UB)	philodendroid
Tribe Zantedeschieae		
Zantedeschia		
Z. albo-maculata (Hook.) Baill.	Brazil. Cultivated at São Paulo, *Gonçalves 769* (UB)	philodendroid
Z. aethiopica (L.) Spreng.	Brazil. Cultivated at University of São Paulo, *Gonçalves 770* (UB)	philodendroid
Z. rehmannii Engl.	Brazil. Cultivated at Brasília, sent by Robert McClure (Australia), *Gonçalves 771* (UB)	philodendroid
Tribe Thomsonieae		
Amorphophallus		
A. bulbifer (Roxb.) Blume	Brazil. Cultivated at São Paulo, sent by Wilbert Hetterscheid (Netherlands), living collection HAM 136, *Gonçalves 742* (UB)	colocasioid
A. konjac C. Koch	Brazil. Cultivated in São Paulo, sent by Krzysztof Kozminski (U.S.A.), *Gonçalves 772* (UB)	colocasioid
A. paeoniifolius (Dennst.) Nicolson	Brazil. Cultivated in Brasília, *Gonçalves 122* (UB)	colocasioid
Pseudodracontium		
P. lacourii (Linden & André) N. E. Br.	Brazil. Cultivated in Brasília, sent by Wilbert Hetterscheid (Netherlands), living collection HAR 74, *Gonçalves 128* (UB)	colocasioid

Table 1. Continued.

Taxa	Source	Collenchyma pattern at the midpoint between base and apex of the petiole
Tribe Peltandreae		
Peltandra		
P. virginica (L.) Kunth	U.S.A. Michigan: *Case & Case s.n.* (UB)	colocasioid
Typhonodorum		
T. lindleyanum Schott	Brazil. Cultivated at University of São Paulo, *Gonçalves 768* (UB0	colocasioid
Tribe Ambrosineae		
Ambrosina		
A. bassii L.	Italy. Sardinia: *F. Ceni 461* (UB)	collenchyma absent
Tribe Areae		
Arum		
A. italicum Mill.	Brazil. Cultivated in Brasília, *Gonçalves 773* (UB)	colocasioid
Dracunculus		
D. vulgaris Schott	Brazil. Cultivated in Brasília, sent by Robert McClure (Australia), *Gonçalves 774* (UB)	colocasioid
Helicodiceros		
H. muscivorus (L. f.) Engl.	Brazil. Cultivated in Brasília, sent by Robert McClure (Australia), *Gonçalves 775* (UB)	colocasioid
Typhonium		
T. giganteum Engl.	Brazil. Cultivated at Belo Horizonte Botanical Garden, sent by Robert McClure (Australia), *Gonçalves 781* (UB)	colocasioid
T. roxburghii Schott	Brazil. Cultivated in Ceará, *Gonçalves 779* (UB)	colocasioid
T. blumei Nicolson & Sivad.	Brazil. Cultivated at Belo Horizonte Botanical Garden, *Gonçalves 777* (UB)	colocasioid
T. venosum (Dryand ex Aiton) Hett. & P. C. Boyce	Brazil. Cultivated in Brasília, sent by Robert McClure (Australia), *Gonçalves 780* (UB)	colocasioid
Tribe Arisaemateae		
Arisaema		
A. dracontium (L.) Schott	Brazil. Cultivated in Brasília, sent by Victor Soukoup (U.S.A.), *Gonçalves 778* (UB)	colocasioid
Pinellia		
P. tripartitia (Blume) Schott	Brazil. Cultivated in Brasília, sent by James Waddick (U.S.A.), *Gonçalves 776* (UB)	colocasioid
Tribe Colocasieae		
Alocasia		
A. cucullata (Lour.) Schott	Brazil. Cultivated in Brasília, *Gonçalves 750* (UB)	colocasioid
A. macrorrhizos (L.) Schott	Brazil. Cultivated at University of Brasília, *Gonçalves 751* (UB)	colocasioid
Colocasia		
C. esculenta Schott	Brazil. Cultivated in Amapá, *Gonçalves 494* (UB)	colocasioid
C. gigantea Hook. f.	Brazil. Cultivated at Belo Horizonte Botanical Garden, *Gonçalves 752* (UB)	colocasioid
Tribe Pistieae		
Pistia		
Pistia stratiotes L.	Brazil. Mato Grosso do Sul: *Gonçalves 749* (UB)	colocasioid

* Here included in the philodendroid pattern with some reservation. See text for more information.

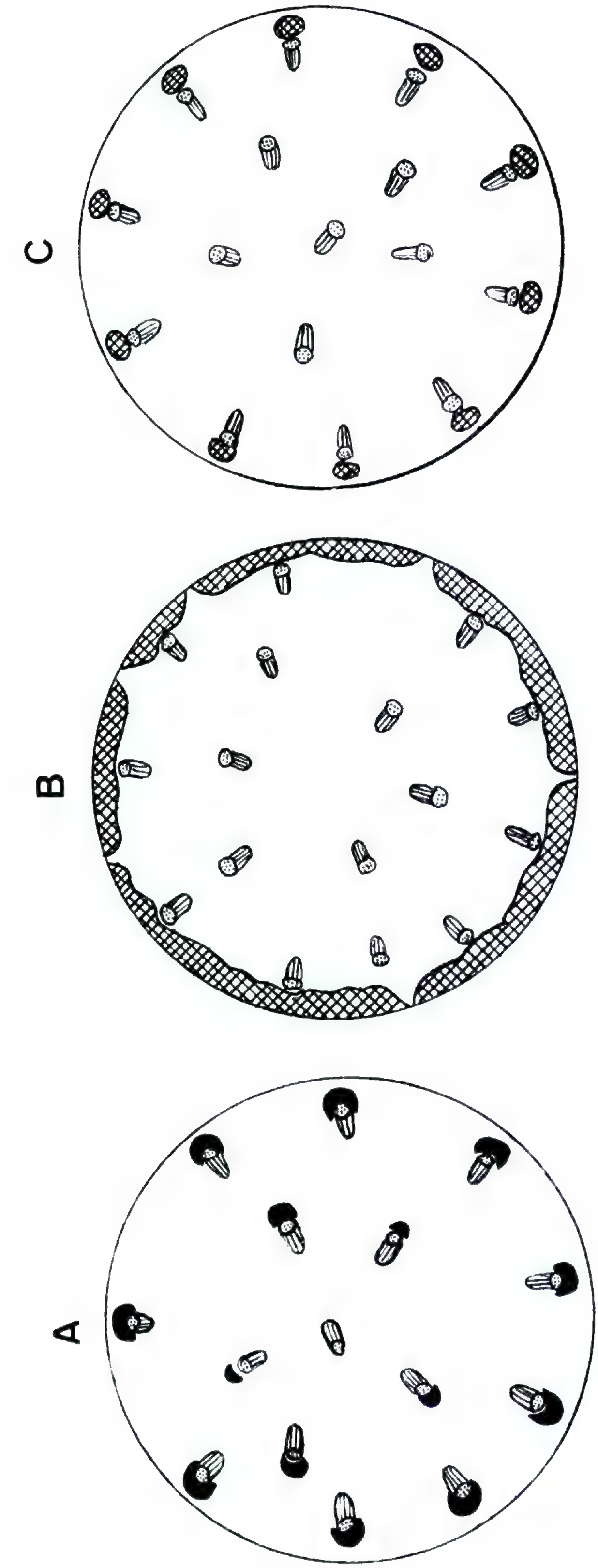
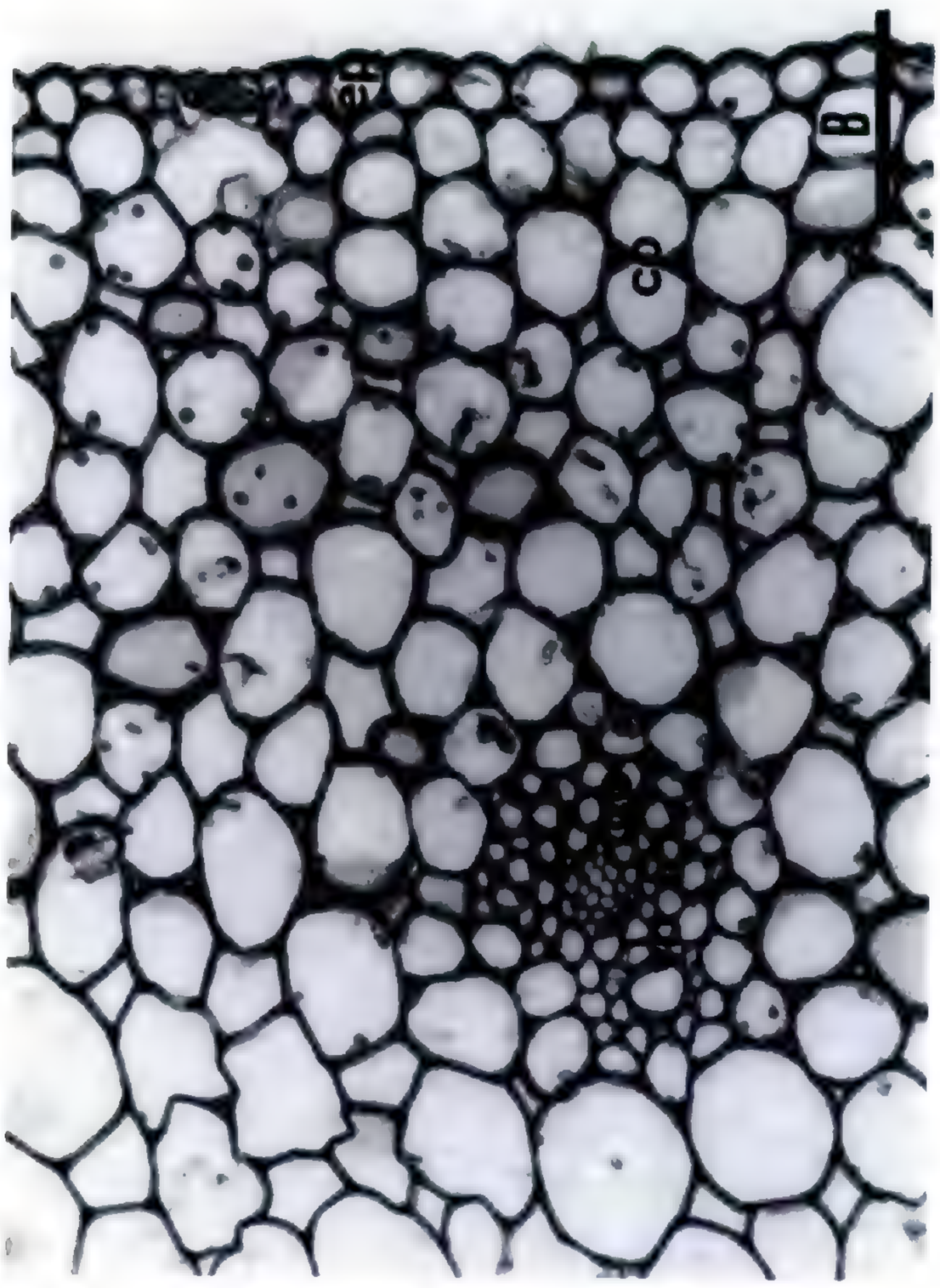


Figure 1. Diagrammatic transversal sections of the petioles showing the main patterns of collenchyma found in the Araceae. —A. Collenchyma absent at the midpoint between petiole base and apex. —B. Philodendroid pattern. —C. Colocasioid pattern.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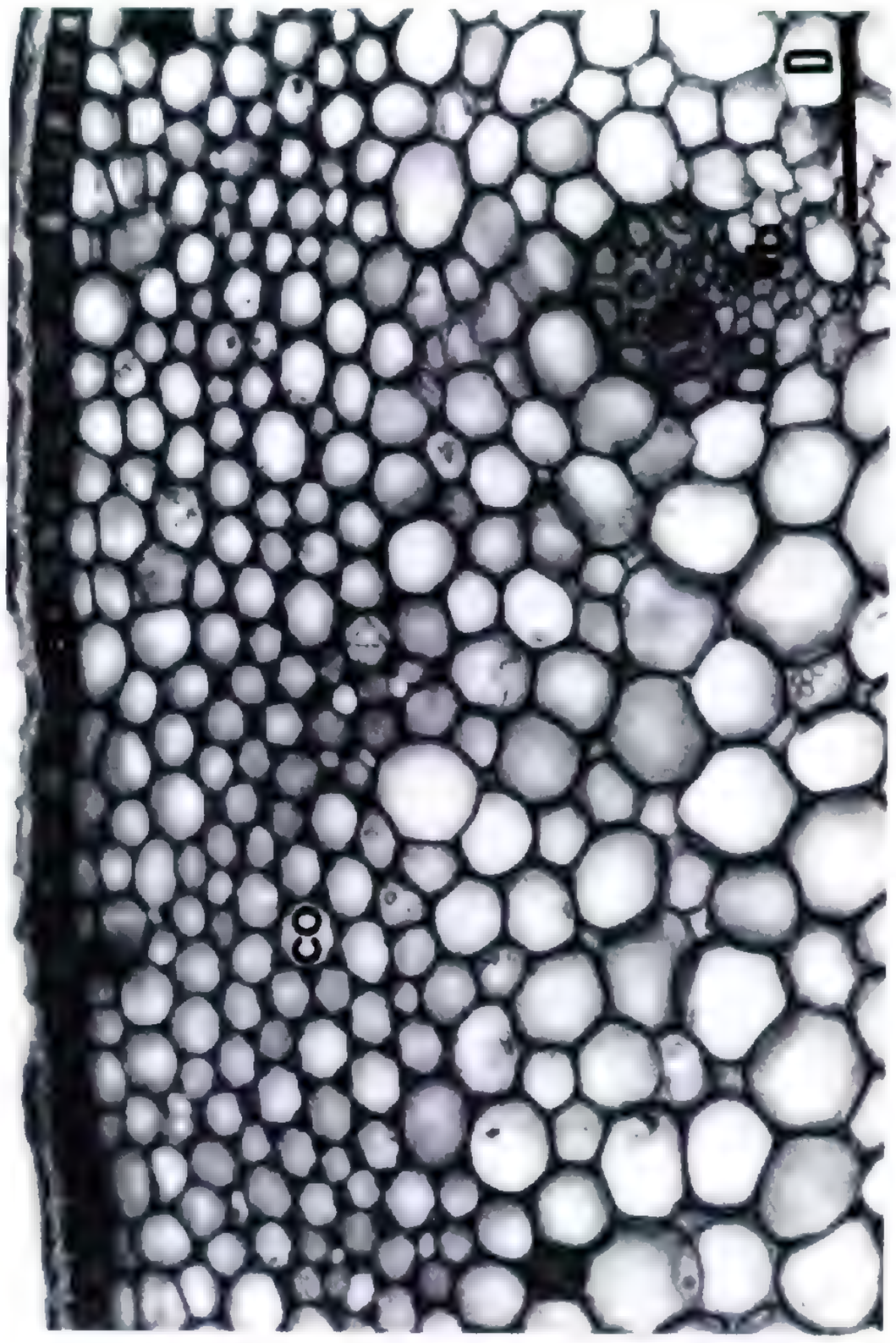
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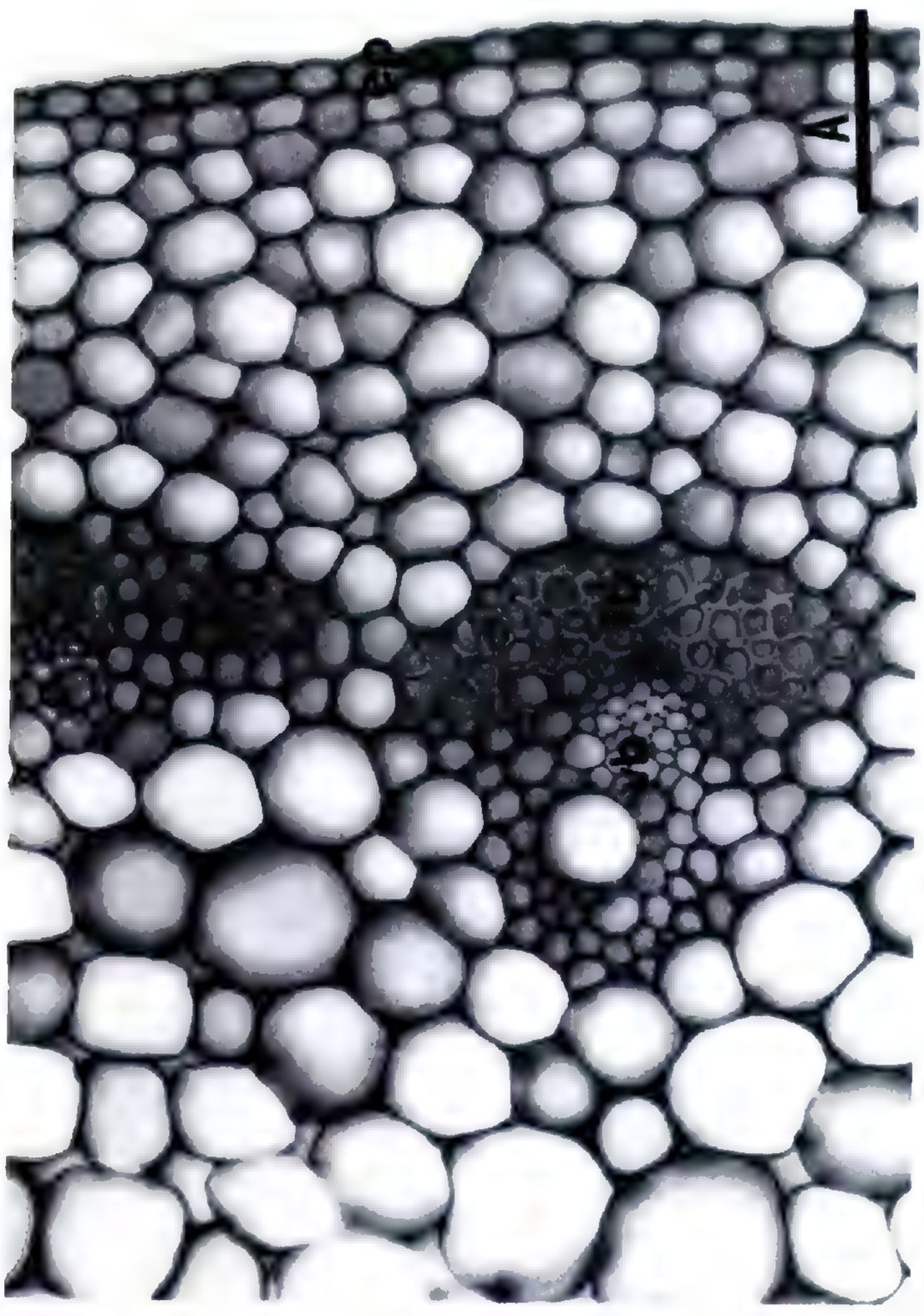
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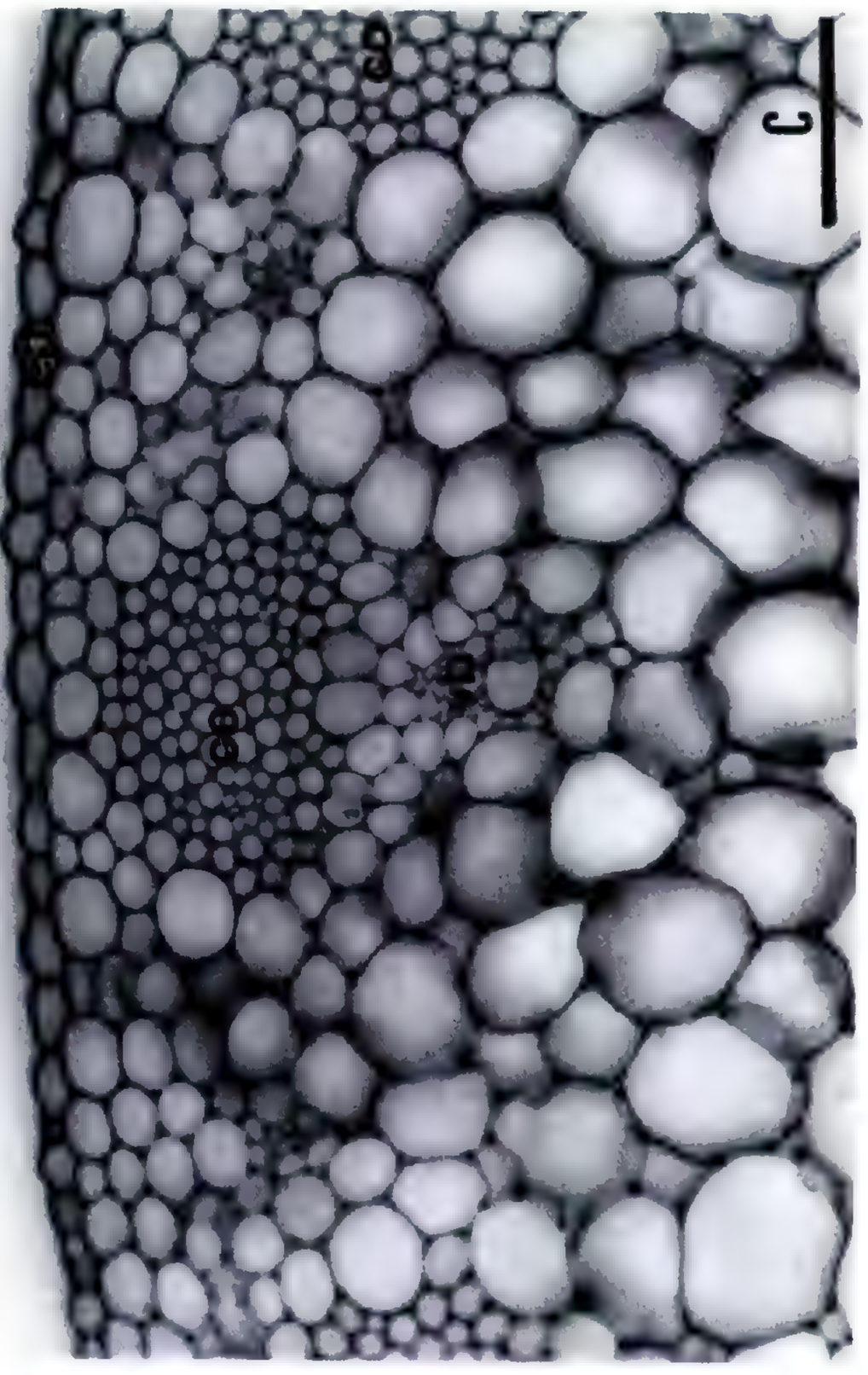
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fenbachia paludicola), or may be in direct contact with the epidermal cells (e.g., *Mangonia tweeediana*, *Homalomena wendlandii*, and *Asterostigma riedelianum*). The thickness of the collenchyma (as well as the number of cell layers on it) is a variable feature among genera and also among species from the same genus. In *Dieffenbachia paludicola*, the thickness of the collenchyma ring ranges from 4 to 10 cell layers, and appeared to be thicker in bigger leaves.

In the genera *Dieffenbachia* (3 species), *Philodendron* (11), *Homalomena* (2), *Aglaonema* (4), and *Zantedeschia* (3), and all surveyed genera from the tribes Spathicarpeae (8 genera, 13 species), Nephthytideae (2, 2), and Montrichardieae (1, 1), as well as in the genus *Schismatoglottis* (2), the collenchyma forms a cortical ring (philodendroid pattern), which can be continuous (as in *Mangonia tweedieana*, *Taccarum weddellianum*, and *Asterostigma cryptostylum*) or segmented by intrusions of parenchyma. These intrusions may be narrow (1 to 4 cell layers) as occur in *Dieffenbachia elegans* and some *Philodendron* species (e.g., *P. uliginosum* and *P. pedatum*) or wider, as observed in *Aglaonema modestum* (up to 8 cell layers). The Asian genus *Aglaonema* deserves special mention. In three of the four sampled species of *Aglaonema* (*A. commutatum*, *A. modestum*, and *A. costatum*) the cortical ring of collenchyma is so widely interrupted that the segments can be classified as strands. However, since they are not associated with vascular bundles, we prefer to assign this genus as having a philodendroid pattern. In any case, *Aglaonema crispum* has a "typical" philodendroid pattern, showing a segmented cortical ring of collenchyma.

It was observed that the position of the parenchyma intrusions usually coincides with the occurrence of stomata in the epidermis in all species in which they occur. Such an aspect needs further investigation in order to verify how permeable to air diffusion is the collenchyma.

In genera with rounded strands of collenchyma (colocasioid pattern) as in all surveyed Areae (2 genera, 7 species), Peltandreae (2, 2), Caladieae (4, 14), Colocasieae (2, 4), Arisaemateae (2, 2), Cryptocoryneae (1, 1), and Zomicarpeae (1, 1), each collenchyma strand is associated with vascular tissues. Such strong association (31 sectioned taxa) may suggest that the vascular bundles share in the ontogenesis of their associated collenchyma strand.

In those genera of subfamily Aroideae in which the collenchyma is absent at the mid regions of the petiole, two different conditions were observed. In *Zamioculcas*, *Gonatopus*, and *Anubias*, there is sclerenchyma associated with the vascular bundles as in all surveyed genera with bisexual flowers (e.g., *Anthurium*, *Monstera*, etc.). In *Ambrosina* no supporting tissue, collenchyma or otherwise, could be observed in the petioles.

Discussion

Based on the patterns of collenchyma, our studies do not support the distinction of subfamilies Colocasioideae, Aroideae, and Philodendroideae, as formulated by Engler and Krause (1920) and later by Grayum (1990) as well as Bogner and Nicolson (1991). This conclusion was reached previously by Mayo et al. (1997) using cladistic analysis of morphological and anatomical characters, as well as by French et al. (1995) using analysis of restriction fragments of chloroplast DNA. The subfamily Aroideae (in its broad sense) can here be circumscribed as including plants with a fully collenchymatous petiole, in a philodendroid or colocasioid pattern. Exceptions are the small tribe Zamioculcadeae (both *Gonatopus* and *Zamioculcas*), *Anubias* (Anubiadeae), and *Ambrosina* (Ambrosineae), in which the absence of collenchyma is here stated as secondary.

Distribution of the colocasioid and philodendroid patterns within the Aroideae seems to support the two major clades proposed by French et al. (1995). All genera herein belonging to French's clade with Grayum's Philodendroideae minus *Peltandra* alliance plus Zamioculcadeae plus *Stylochaeton* have a philodendroid pattern of petiolar collenchyma. The only exceptions are the African tribe Zamioculcadeae and the African genus *Anubias*. The surveyed genera from French's clade with Grayum's Aroideae plus *Peltandra* alliance plus Colocasioideae have a colocasioid pattern of petiolar collenchyma. The exceptions are *Ambrosina*, in which the collenchyma seems to be absent, and *Schismatoglottis*, in which the collenchyma is clearly philo-

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Figure 2. Transversal sections of the petioles. *Epipremnum pinnatum*:—A. Midpoint, between petiole base and apex. —B. Pulvinar region. *Philodendron cipoense*:—C. Midpoint, between petiole base and apex. *Syngonium angustatum*:—D. Midpoint, between petiole base and apex. (Scale bars = 100 μm; ep = epidermis, fb = fibers, vb = vascular bundle, co = collenchyma.)

dendroid. Interestingly, the tribe Schismatoglottideae (five genera, only *Schismatoglottis* here surveyed) comprises the most basal clade within the huge Aroideae plus *Peltandra* alliance plus Colocasieae clade published by French et al. (1995), together with the clade *Cryptocoryne* plus *Lagenandra*.

In contrast, the African genera *Gonatopus* and *Zamioculcas* (tribe Zamioculcadeae) do not have collenchyma in the petioles, and sclerenchyma comprises the main supporting tissue (although the collenchyma can occur in the apex and base of petioles or in the median pulvinus of *Gonatopus*). Both Old World genera *Gonatopus* and *Zamioculcas* were earlier placed in subfamily Pothoideae (Engler, 1905), but were later excluded and added to Lasioideae by Bogner and Nicolson (1991). Mayo et al. (1997) moved both genera to the huge subfamily Aroideae, accommodating them in tribe Zamioculcadeae. Moreover, both genera possibly branched early in the evolutionary history of the Aroideae (Mayo et al., 1997). An alternative hypothesis concerns their habitat. Both genera occur in southeastern Africa and are subjected to strongly seasonal rainfall. A secondary loss of the collenchyma to increase drought resistance is one possible explanation for its absence. Well-developed sclerenchyma is thought to reduce the injurious effect of wilting in the leaves of xerophytic plants (Esau, 1977).

Another African genus in which collenchyma is restricted to the apical pulvinus is *Anubias*. We surveyed two species (*A. afzelii* and *A. hastifolia*), and both have sclerenchyma as the main supporting tissue. Since *Anubias* is not considered a basal taxon within the philodendroid clade (see French et al., 1995), we consider that the fully collenchymatous petioles were secondarily lost.

The absence of collenchyma in *Ambrosina* can also be explained as a secondary loss. The monotypic genus *Ambrosina* comprises diminutive plants (Mayo et al., 1997), and their very reduced size may make the presence of supporting tissues in the petioles less adaptively significant. Further, most of the length of the petiole remains under the soil.

In some genera with bisexual flowers (and also in *Zamioculcas*, *Gonatopus*, and *Anubias*) some collenchyma may occur at the base and at the apex of petioles (Fig. 2B). This occurs mainly when a pulvinus is present (French, 1997). This collenchymatous portion at the apices and bases can be found even when there is no morphologically distinct pulvinus. Such areas allow some plasticity to fully developed leaves. It is possible that the fully collenchymatous petiole of the monoecious genera arose in consequence of an increased development of the pulvinus. It is noteworthy that in the transition zone between petiole-leaf blade, the sclerenchyma is always absent (or dramatically reduced), whether or not the collenchyma is present. In some genera (e.g., *Zamioculcas*, *Epipremnum*) there is also a basal pulvinus that can be morphologically distinct or not. In this case, the anatomical structure at the base is similar to that of the apical pulvinus.

The monoecious genera have been considered to be phylogenetically more derived than the genera with bisexual flowers (French et al., 1995; Mayo et al., 1997). Since the presence of a fully collenchymatous petiole seems to coincidentally appear only in more derived genera of Araceae, its occurrence probably represents an apomorphic feature in this family.

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VEGETATIVE ANATOMICAL DATA AND ITS RELATIONSHIP TO A REVISED CLASSIFICATION OF THE GENERA OF ARACEAE[1]

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Abstract

A recent compilation of anatomical literature and original anatomical investigations of the leaf and petiole of Araceae led to a search for the most concise systematic organization of the genera within this family. Among structural data sets summarized, useful observations included those of type and position of conducting and mechanical tissue, aerenchyma, raphide crystals, and laticifers. These data were superimposed on three lines of evidence using DNA sequences. The revised classification presented here resulted in fewer anomalous generic placements and provides a framework for understanding the evolution of the family. Currently 106 genera are recognized and divided among 9 subfamilies and 21 tribes. The new subfamily Schismatoglottidoideae is described.

Key words: anatomy, Araceae, DNA sequence, Lemnaceae, Schismatoglottidoideae taxonomy.

Our current image of the family Araceae was established by Schott (1860), who assembled the genera that we now call aroids. His classification was based mostly on reproductive characters (see Grayum, 1990, for a thorough review). Generic classification of the Araceae was refined during the 19th and early 20th centuries by Engler, whose last arrangement (Engler, 1920) was based on decades of accumulated data. The standard he set was ahead of its time in being based on a broad and inclusive array of combined morphological and anatomical observations, both reproductive and vegetative. His keys and descriptions utilized habit, leaf arrangement and shape, leaf venation patterns in considerable detail, type of laticifers and relationship to veins, mechanical tissue including distribution of trichosclereids, inflorescence characters, floral parts, their shapes and fusions, ovary locules, and ovule position. His classification stood for about 50 years, and students of the family have traditionally followed this broad "Englerian" approach to classification issues (cf. Grayum, 1990).

Also in this category is a classification for Japan and adjacent areas by Hotta (1970), whose Englerian approach was later documented in detail (Hotta, 1971). Bogner's (1979) presentation of Engler's classification updated the changed generic concepts occurring in intervening time. Similarly, Bogner and Nicolson (1991) continued this work, removing *Acorus* from the family (see Grayum, 1987), and producing useful keys that invoked a wide variety of reproductive and vegetative characters. A half dozen additional rearrangements in tribal positions were proposed. Incrementally, Engler's infrastructure was evolving.

Hutchinson's (1973) arrangement emphasized mostly reproductive characters in the spirit of Schott and Hooker. His suprageneric infrastructure subdivided the family into 18 tribes, an approach not recognized by modern workers.

Comparisons of several classifications since Engler (1920) have been published by Nicolson (1988), Croat (1990), Mayo et al. (1997), and Keating (2002). These comparisons contrasted varying concepts of aroid generic infrastructure and will not be repeated here. Most frequently, groupings of genera into tribes or adjacent tribes are less controversial, but there remain substantial differences in recognition of subfamilies, their generic scope, and their relative position. Subfamily relationships are especially important to understand as they represent the base of evolutionary branches within the family and point to the character of its early divergence. Determining these relationships using structural characters is hampered by lack of understanding of all instances of parallel evolution and character reversals. For instance, Hotta (1971) noted that tuberous growth, the climbing habit, and

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compound leaf formation have arisen independently among the several subfamilies.

In the 1980s, a number of anatomical contributions based on large generic samples were published by French and collaborators (French, 1985a, b, 1986a, b, c, 1987a, b, c, 1988; French & Tomlinson, 1980, 1981a, b, c, d, 1983, 1984; see review by French, 1997). These yielded a wealth of comparative data requiring integration into an updated view of generic evolutionary relationships. Grayum (1990) provided a thorough review of useful characters and proposed a revised classification, which he claimed returns somewhat to pre-Englerian concepts; that is, he makes the point that genetic isolation begins with modification of reproductive organs, and that we should be paying more attention to these structures and to pollination systems. Still, he was comprehensive in his approach to data analysis.

A compilation of vegetative anatomical data, including original observations, has been assembled by Keating (2000, 2002, 2003, 2004). These studies had three goals: understanding the limits of variation of histological complexity, assessing the potential of such data in understanding evolutionary trends of specialization, and assessing their potential to be useful in delineating generic and suprageneric categories.

As the project progressed, there arose the need to choose a classification against which to arrange the growing files of observations. The anatomical trends compared against classifications produced up to 1995 yielded a number of anomalies that made the choice difficult. Originally I had hoped to use the classification of Mayo et al. (1997), but their decision not to recognize several formal categories pending ongoing studies provided insufficient hypotheses for testing the relationship of anatomical data to a full classification. For example, their large subfamily Aroideae, containing 74 genera, included a group of 27 genera that are scattered among "alliance" and "no alliance" tribal groupings. Here, those genera are placed in the subfamily Philodendroideae based primarily on possession of banded or banded-interrupted (types B, Bi, or Sb) collenchyma (see Keating, 2000, table 3).

While this decision was pending, French et al. (1995) published an analysis of cpDNA restriction site data that included a sample of 85 currently accepted genera. Their resulting consensus tree reinforced a number of traditional concepts regarding the scope and recognition of subfamilies and tribes, while also promoting new ways of conceiving of some relationships. It became the obvious candidate against which to order the anatomical data. The above-mentioned ordering of the 27 philodendroid genera exactly corresponded with the cpDNA topology.

After the present contribution had been drafted, I received consensus and bootstrap trees for the family from Cabrera et al. (2003). They have completed sequencing two genes, *rbc*d and *mat*K, for 94 taxa, and which included 3335 molecular characters. Their topology resulted in a few generic shifts in position from the French et al. (1995) results, which will be discussed in the context of subfamilies and tribes below. At final editing, I received a copy of the work by Rothwell et al. (2004) based on sequence data of the chloroplast *trn*L-*trn*F intergeneric spacer. Thirty-six species of Araceae and Lemnaceae were sampled for a study that dealt especially with the relative positions of Lemnaceae and *Pistia*.

After reviewing all contemporary classifications, the approach toward developing this revision involved (1) comparing anatomical data sets against DNA sequence data; (2) inserting in correct sequence various genera that had not been sampled [their placement was not controversial when reviewing Mayo et al. (1997) and other classifications]; (3) determining the level of recognition of generic groupings; and (4) checking anatomical, morphological, and geographic data for anomalies or evidence of unparsimonious suprageneric concepts.

The resulting classification (Appendix 1) appears to reduce the need for unnecessary ad hoc hypotheses of evolutionary relationships. French et al. (1995) did not revise the classification of the family after presenting their cpDNA tree. Also, some of their more interesting conclusions were not adopted in the new classification by Mayo et al. (1997), although, to some degree, it influenced their generic sequence.

Nomenclatural sources for family infrastructure taxa in Appendix 1 include Kubitzki (1998), Landolt (1998), Mayo et al. (1997), Nicolson (1984), and J. L. Reveal's nomenclatural database (<www.inform.umd.edu/pbio/fam>). The genera (marked *) not sampled by French et al. (1995) were inserted in Appendix 1 following the recent classifications cited above and after checking the evidence for anomalous anatomy.

Comments on Family Infrastructure

Some of the anatomical characters summarized in the following systematic discussion are coded

using typology that is defined in Appendix 2 and in detail in Keating (2002).

The first five subfamilies contain genera possessing bisexual flowers.

SUBFAMILY GYMNOSTACHYDOIDEAE

This subfamily contains the eastern Australian genus *Gymnostachys*, whose isolated taxonomic position is easily justified. Vascular bundles are unique, having fibers that ensheath the bundles with unusual cap and girder architecture. Collenchyma is absent.

The molecular genetic evidence indicates that the genus clusters on the same branch with the genera of Orontioideae, although structural data suggest no such position. Its vasculature and undifferentiated mesophyll structure resemble that of no other aroids. With the removal of *Acorus* from the family, *Gymnostachys* is the only remaining genus with linear leaves and parallel-organized stomata. This and other unusual anatomy, especially the unique form of leaf vascular bundles would formerly have suggested its separation from the family.

SUBFAMILY ORONTIOIDEAE

This subfamily is divided into two tribes. The tribe Orontieae, containing only the eastern North American genus *Orontium*, has acrodromous leaf venation, phloem fiber caps, collenchyma absent, laticifers non-anastomosing, and raphide cells bearing multiple crystal bundles.

Tribe Symplocarpeae, containing *Lysichiton* of western North America, eastern Asia, and Japan, and *Symplocarpus* of eastern North America, eastern Asia, and Japan, has leaves with pinnate venation, fibers absent, collenchyma types C and B, and laticifers absent.

Molecular genetic evidence affirms the single subfamily concept with *Orontium* being less closely related to the other two genera. On this basis, and on account of structural data, tribal-level recognition is warranted to reflect this distinction. Mayo et al. (1997) do not recognize tribes in this subfamily.

SUBFAMILY POTHOIDEAE

The 16 genera included here occur in the tropics of Asia, Malaysia, Madagascar, and the Americas, and Africa in the case of *Rhaphidophora*.

Tribe Pothoeae, containing *Pothos*, *Pedicellarum*, *Pothoidium*, and *Anthurium*, has leaves and petioles with type I vascular bundles; fibers ensheathing vascular bundles; collenchyma absent; and laticifers absent. Trichosclereids are encountered only rarely in *Pothos*.

Tribe Monstereae includes the 12 genera *Holochlamys*, *Spathiphyllum*, *Rhodospatha*, *Stenospermation*, *Scindapsus*, *Rhaphidophora*, *Anadendrum*, *Monstera*, *Alloschemone*, *Epipremnum*, *Amydrium*, and *Heteropsis*. Anatomically, these genera share types I and II vascular bundles; fibers ensheathing vascular bundles or occurring as bundle caps; trichosclereids in 9 of the 11 genera; collenchyma type B or absent.

Grayum (1990) proposed this subfamily concept but others have divided the genera among the Pothoideae and an adjacent subfamily Monsteroideae (Mayo et al., 1997; Bogner & Nicolson, 1991). The latter authors noted a lack of clear character distinctions supporting two subfamilies and also suggested that the genera could be united.

On the basis of all structural and molecular genetic evidence, no basis can be discerned to justify subfamily-level distinction for the two included tribes. For tribal separation, presence versus absence of collenchyma stands out as well as more leaf variation in the Monstereae. The trichosclereid-bearing genera have a strong tendency to be grouped in the Monstereae. That line of evidence is weakened by the rare presence of trichosclereids found in the petiole of one *Pothos* species and the fact that two genera of tribe Monstereae, *Amydrium* and *Heteropsis*, have none. In summary, even tribal diagnostic differences are indicative but not strong.

SUBFAMILY LASIOIDEAE

The 10 included genera occur in the American and Asian tropics, the Malay archipelago, and Africa in the case of *Lasimorpha*. The genera are: *Cyrtosperma*, *Lasimorpha*, *Podolasia*, *Lasia*, *Anaphyllum*, *Urospatha*, *Anaphyllopsis*, *Pycnospatha*, *Dracontium*, and *Dracontioides*. Vascular bundles are types I and II, fibers ensheath bundles or occur as bundle caps, collenchyma is type B or absent, and the petiole usually develops type 4 air cavities, an uncommon type within the Araceae.

Further tribal infrastructure in this subfamily is unnecessary, as the morphology and anatomy of the genera are distinct and uniform; in fact, as defined here, the subfamily constitutes one of the more uniform groupings in the Araceae. Mayo et al. (1997) agreed, as did Grayum (1990), who, however, added the orontioid genera. The orontioids do not fit here in terms of leaf type (elliptic) and petiole aerenchyma (type 3 only).

Bogner and Nicolson (1991) established an expanded subfamily concept, highly variable in terms of vegetative and floral characters, that included 8 tribes and 23 genera. Included are the bisexual-

flowered group, the orontioids, and the African genera *Gonatopus*, *Zamioculcas*, *Nephthytis*, *Anchomanes*, and *Pseudohydrosme*. Their tribe Lasieae (herein subfamily Lasioideae) subtribe Dracontiinae (plants with perigone) holds nine genera, and subtribe Pycnospathinae (no perigone) includes solely *Pycnospatha* in their Lasioideae. Superficially, the habit and leaves are similar in the African genera, as is their possession of banded collenchyma, and types I and II vascular bundles. However, the African genera often have laticifers or ducts, and biforines or biforine-like raphides, which are absent in the core lasioids as defined here. In my opinion, Bogner and Nicolson's subfamily concept is polyphyletic based on molecular and current structural evidence.

Supporting a restricted concept of Lasioideae are studies by Seubert (1993, 1997) describing the distinctive, ornamented lasioid seeds, and the work of Hay (1992) on biogeography of the Lasieae that suggests a separate and prolonged evolutionary history for this group of genera.

SUBFAMILY CALLOIDEAE

The sole genus is the circumboreal herb *Calla*. This rooted aquatic has a fully expanded spathe, a more or less uniform spadix that includes bisexual flowers without perigone, a petiole sheath with extended apical ligule, the cordate-pinnate leaves with higher-order parallel, arcuate veins merging toward the margin, and petiole with type 3 aerenchyma. Vascular bundles are types I and II, collenchyma is absent, and laticifers are non-anastomosing.

The cpDNA tree (French et al., 1995) confirms its isolated position, as does its unique combination of boreal range, plus morphological and anatomical factors. Bogner and Nicolson (1991) and Hotta (1970) agreed with this circumscription. Uniquely in the history of this genus, the consensus tree for *rbc*d and *mat*K genes (Cabrera et al., 2003) suggests placement of *Calla* on an isolated arm between the schismatoglottids and the subfamily Aroideae. Grayum (1990) had included *Calla* in a large subfamily concept containing 40 genera, which are distributed among four of my subfamilies.

The remaining 75 genera have unisexual flowers and are monoecious. Mayo et al. (1997) considered them to be monophyletic and sufficiently closely related to constitute a single subfamily Aroideae (see table 3, Keating, 2000). However, within that large grouping, structural data, together with the cpDNA tree topology, and the numbers of restriction site changes, provide additional support for subfamily-level recognition for the taxa that follow.

SUBFAMILY PHILODENDROIDEAE

This subfamily includes seven tribes and 27 genera. Vascular bundles are types I and II, fibers occur as phloem caps, secretory ducts are present or absent, and laticifers are non-anastomosing. The best anatomical character uniting this group is collenchyma occurring as types B and Bi. While the strict consensus tree for *rbc*d and *mat*K genes displays unresolved relationships of the tribal groupings, the cpDNA tree indicates a common origin for the included genera and provides the framework for the sequence that follows. Together these genera constitute the most structurally diverse subfamily.

Tribe Philodendreae includes five closely related genera of the American and African tropics, southeast Asia, and Malaysia: *Montrichardia*, *Anubias*, *Furtadoa*, *Philodendron*, and *Homalomena*. In addition to the cpDNA results, all are marked by a rare character, shared by only two genera of the tribe Culcasieae, possession of sclerotic hypoderm in the roots (French, 1987c). In other recent systems, the five genera of Philodendreae are scattered among various tribes and subfamilies, probably due to structural variations. Laticifers and ducts are often present, but vascular bundles, aerenchyma, and leaf venation and stem habit are all variable (Keating, 1997). The sequence data of Cabrera et al. indicate some isolation between *Montrichardia* and the other four genera.

Tribe Zantedeschieae, including *Zantedeschia* of southern Africa and *Callopsis* of eastern Africa, has banded-interrupted collenchyma, not a common type. These genera are placed in separate tribes in most schemes and they differ in diagnostic characters of their anatomy: *Zantedeschia* lacks fibers, has parallel intersecondaries in the leaf, elongated raphide cells and biforine-like raphides, type III vascular bundles, and type 3 aerenchyma. *Callopsis* lacks fiber caps as well as the other characters. The *rbc*d and *mat*K sequences would support tribal-level separation. On the other hand, the cpDNA tree suggests a close relationship.

Tribe Stylochaetoneae, including the African genus *Stylochaeton*, has perigoniate flowers, a character it shares with the next tribe, Zamioculcadeae. *Stylochaeton* is easily distinguished from the next two genera in having type 3 aerenchyma, biforine raphides, and fibers absent. These two tribes, and tribe Zantedeschieae, share the same long branch on the cpDNA tree. Cabrera et al. (2003) show this tribe as being closely allied to the following tribe.

Tribe Zamioculcadeae contains the genera *Gonatopus* and *Zamioculcas* of southeast Africa. They have fibers as phloem caps, variable collenchyma (types B, Bi), secretory ducts present or absent, styloids occasional, and elongated raphide cells. In the cpDNA tree, the tribe is at the end of a clade having 29 additional restriction site changes and a number of structural differences. This is consonant with the clustering found in the *rbc*d and *mat*K gene consensus tree. In earlier classifications, the tribes Zamioculcadeae (*Gonatopus* and *Zamioculcas*) and Stylochaetoneae (*Stylochaeton*) have been placed in about six different subfamilies, but they are at home in the present concept of subfamily Philodendroideae.

The leaf of *Stylochaeton* is simple while those of *Gonatopus* and *Zamioculcas* are pinnately compound. *Stylochaeton* has type 3 aerenchyma while *Gonatopus* and *Zamioculcas* have only compact aerenchyma. *Gonatopus* and *Zamioculcas* have occasional styloids. The three genera also vary in habit but are the only monoecious genera of Araceae with perigoniate flowers.

Tribe Aglaonemateae includes the African genera *Nephthytis*, *Anchomanes*, *Pseudohydrosme*, and the southeast Asian and Malaysian genera *Aglaonema* and *Aglaodorum*. They have fibers, well-developed as bundle sheaths or caps, collenchyma of types B, Bi, and Sb, and non-anastomosing laticifers. They have been placed in two tribes and there are some differences to support this, including contemporary geographic separation, although *Nephthytis* occurs throughout the tribal range. There are differences in leaf shape. Similarities include the presence of type Sb collenchyma, a rare occurrence in the Araceae, and the presence of biforine raphides. Combined molecular genetic evidence and the collenchyma development support the present concept.

Tribe Culcasieae includes the tropical African genera *Culcasia* and *Cercestis*. They have type I vascular bundles, type B collenchyma, and secretory ducts. In the roots, they possess a sclerotic hypoderm with septate fibers, and resin canals, all features shared by at least some members of the tribe Philodendreae. The genera are isolated on the same branch of trees using molecular genetic evidence and appear classified together by Mayo et al. (1997). Grayum (1990) placed them in adjacent tribes in this subfamily, while Bogner and Nicolson (1991) placed the adjacent tribes in subfamily Lasioideae. Raphides, leaf shape, collenchyma, aerenchyma, and fibers all support their close relationship and placement within the Philodendroideae.

Tribe Spathicarpeae includes 10 tropical and subtropical American genera: *Bognera*, *Dieffenbachia*, *Spathantheum*, *Gorgonidium*, *Synandrospadix*, *Gearum*, *Spathicarpa*, *Asterostigma*, *Mangonia*, and *Taccarum*. They share variable vascular bundle form (types I, II, III), fibers ensheathing bundles or as bundle caps, collenchyma type B, laticifers with transparent contents, non-anastomosing, or absent. All recent systems (Grayum, 1990; Bogner & Nicolson, 1991; Mayo et al., 1997) and gene sequence evidence agree on a close relationship for these genera. The presence of laticifers with transparent contents is diagnostic.

The subfamily Philodendroideae embodies the most diverse set of character states in the family, and not just due to the inclusion of the huge and character-rich genus *Philodendron*. Considering this diversity, the subfamily remains coherent because of the type B collenchyma and derivative types and the molecular data.

SUBFAMILY SCHISMATOGLOTTIDOIDEAE

This subfamily, containing two tribes and seven genera, is recognized for the first time (Appendix 3). The plants are mostly evergreen herbs, mostly aquatic or amphibious with simple, pinnately veined leaves. Their spadices have unisexual flowers separated by a naked or sterile flower zone, usually without a sterile appendix. Pollen are almost entirely psilate and inaperaturate.

Most genera have representatives in Borneo or Brunei. In addition, *Schismatoglottis* ranges in Malaysia and southeast Asia and includes three species in South America. *Piptospatha* is found in the Indonesian peninsula. *Cryptocoryne* occurs in south India, Indochina, south China, and the Philippines, Indonesia to New Guinea, and *Lagenandra* ranges from Assam to Bangladesh.

Anatomical features common to the subfamily usually include epidermal cells with straight-sided polygonal walls (surface view) that are large or columnar in transverse section, and brachypara-hexacytic stomata with narrow subsidiary cells. Fewer or more subsidiary cells also occur. Vascular bundles are types II and III. Ground tissue in the petiole or midvein is type 3, or occasionally type 4. The collenchyma pattern is banded or banded-interrupted, approaching stranded in the Cryptocoryneae. However, collenchyma strands appear not to be the more organized type Sv strands as described below for the subfamily Aroideae. A transitional condition, showing the capacity to form both types of collenchyma, has been detected in the schismatoglottid genus *Bucephalandra* (Keating, 2000, 2002). The genus exhibits banded col-

lenchyma in the midrib and more discrete strands in the petiole. Raphide crystals are variable and not useful for distinguishing this subfamily or its tribes. Pollen is reported (Grayum, 1992; Mayo et al., 1997) as inaperturate and psilate. They reported irregularly dimpled pollen in *Hottarum* (now in *Piptospatha*) and rugulate or verrucate pollen in *Schismatoglottis*.

Tribe Schismatoglottideae holds the five genera *Phymatarum*, *Schismatoglottis*, *Aridarum*, *Piptospatha*, and *Bucephalandra* (also see Bogner & Hay, 2000). They occur in Malaysia and southeast Asia, and South America (in the case of *Schismatoglottis*). Fibers as bundle caps are present or absent, nonanastomosing laticifers are present, and collenchyma is type B or Bi. Two pollen nuclei are present at anthesis.

Tribe Cryptocoryneae includes the Asian and Malaysian genera *Cryptocoryne* and *Lagenandra*. They have type Bi collenchyma that may approach the stranded appearance of type Sv as in the subfamily Aroideae as described above. However, they can be distinguished from the latter. Where independent strands appear, they may occur in the absence of vascular bundles as well as occurring aligned with them. Fibers are absent, as are laticifers in the leaves. Three pollen nuclei are reported in these two genera.

The two tribes were first placed adjacent to each other by Mayo et al. (1997) in their *Schismatoglottis* alliance of the subfamily Aroideae. Other recent systems have constituted the tribes as given here, but with separated subfamily placements. Grayum (1990) placed the tribe Schismatoglottideae in the subfamily Calloideae and the *Peltandra* alliance and the tribe Cryptocoryneae in the subfamily Aroideae. Bogner and Nicolson (1991) placed the tribe Schismatoglottideae in the subfamily Philodendroideae and the Cryptocoryneae near the end of their subfamily Aroideae. On the basis of combined molecular genetic topologies, the two tribes exhibit proximity of relationship. Also, anatomical features, especially collenchyma, reflect the same transitional position between the subfamilies Philodendroideae and Aroideae.

SUBFAMILY LEMNOIDEAE

Five genera, *Spirodela*, *Landoltia*, *Lemna*, *Wolffia*, and *Wolffiella*, are included in subfamily Lemnoideae. This group of small, floating plants has type II vascular bundles, no collenchyma or laticifers, but does contain raphide cells. The genera have appeared to form an easily interpreted reduction series, in the above order, beginning with *Spirodela*. However, the strict consensus tree of Rothwell et al. (2004) indicates that *Lemna* is related at a node distal to *Wolffiella*.

The lemnoids have been the subject of a recent detailed review and structural account by Landolt (1998), who accepts family-level recognition. All DNA sequence data indicate that the genera are clearly nested within Araceae. While the plants themselves are very reduced in stature, the anatomical data gathered from them are compatible with the genera clearly being aroids. Stockey et al. (1997) reviewed paleobotanical evidence that lemnoid genera and *Pistia* may be related through the transitional genus *Limnobiophyllum* that occurs in Paleocene and Miocene strata. However, the morphological distance between lemnoids and other aroids as well as the molecular genetic data best indicate subfamily-level recognition, and isolation from *Pistia*.

SUBFAMILY AROIDEAE

This subfamily contains the remaining 8 tribes and 36 genera of Araceae. As defined here they are the most anatomically uniform subfamily. Most importantly, all genera possess true type Sv collenchyma, and are the only genera to do so (Keating, 2000). This type occurs usually as subcircular independent strands always aligned with, and external to, peripheral vascular bundles. Collenchyma strands never appear as closely proximal phloem caps. The genera possess types II and III vascular bundles. Laticifers are usually non-anastomosing, but occur as anastomosing in two tribes, and only in this subfamily. This concept of Aroideae corresponds exactly with the cpDNA tree, and the genera emerge from a single well-resolved clade on the *rbc*d and *mat*K strict consensus tree.

Until recently, the presence of articulated laticifers seemed to unite a group of genera as a single subfamily Colocasioideae. However, the cpDNA tree first provided evidence that articulated laticifer-bearing clades arose independently in the Old World (Colocasieae) and the New World (Caladieae). The tribes are not adjacent on any molecular genetic tree. Earlier, Fox and French (1988) called attention to the presence of sterols in laticifers of the New World *Xanthosoma* and *Syngonium* (tribe Caladieae here), but only sterol esters in the Old World *Alocasia* and *Colocasia* (tribe Colocasieae). In this case, aggregated anatomical data have not been sufficient to separate these groups, an illustration of the difficulties of using structural data in isolation.

Tribe Thomsonieae includes *Amorphophallus* of

Africa, southeast Asia, Malaysia, and northeastern Australia, and *Pseudodracontium* of southeast Asia. Their leaves show tetrahedral branching at the apex of robust, erect petioles, reticulate venation in intercostal areas, and non-anastomosing laticifers. The genera have been traditionally recognized as forming a tribe.

Tribe Caladieae includes 11 genera: *Hapaline*, *Syngonium*, *Xanthosoma*, *Chlorospatha*, *Ulearum*, *Filarum*, *Zomicarpella*, *Caladium*, *Scaphispatha*, *Jasarum*, and *Zomicarpa*. They are South American except for *Hapaline*, which occurs in southeast Asia and Brunei. Phloem fiber caps are common, raphides are variable, including biforines, and anastomosing laticifers are present. The genera of this tribe are often divided into two tribes (Bogner & Nicolson, 1991; Mayo et al., 1997; and Grayum, 1990, in part), but molecular genetic evidence provides no support for further separation or recognition of a tribe Zomicarpeae.

The tribe Arisareae contains *Ambrosina* and *Arisarum* of the Mediterranean region. They have type II vascular bundles, non-anastomosing laticifers, and type 4 petiole aerenchyma. The two genera are often divided into separate tribes but the cpDNA tree provides no support. The two genera apparently share a close common ancestry with the next tribe.

Tribe Peltandreae is interpreted here to include five genera: *Peltandra* of eastern North America, and from Madagascar: *Typhonodorum*, *Colletogyne*, *Carlephyton*, and *Arophyton*. Leaf intersecondaries are numerous and parallel, raphides are biforines and biforine-like cells, laticifers are non-anastomosing, and petiole aerenchyma is type 3. The geographic disjunction is less puzzling when considering fossil evidence. Ancestors of *Typhonodorum* were in North America (Tennessee) during the Eocene, indicated by specimens named *Philodendron limnestes* by Dilcher and Daghlian (1977). They were later considered as belonging in tribe Peltandreae near *Typhonodorum* by Mayo (1991). The trees of Cabrera et al. (2003) suggest a separation of *Typhonodorum* from Peltandreae, but on the basis of microscopic structural evidence, no further rearrangement is undertaken. Together the five genera share a number of leaf characters including biforine raphides and biforine-like cells, non-anastomosing laticifers, and type 3 aerenchyma. There are some variations in histology but not sufficient to recognize separate tribal status.

Tribe Pistieae comprises pantropical floating plants of the genus *Pistia*. Leaf aerenchyma is type 3, collenchyma forms types C and Sv, biforine raphides are present, and laticifers are absent. In spite of the distinctive aquatic life-adapted features of the genus, it fits into the Aroideae according to molecular genetic evidence, and its histology, summarized above, is typical for the subfamily. The type Sv collenchyma strongly confirms this placement. There appears to be no support for separate family status as proposed by Takhtajan (1997).

Tribe Arisaemateae consists of the genera *Arisaema*, widespread across Africa, Asia, and North America, and *Pinellia* of eastern Asia and Japan. Both share leaf secondary venation having brochidodromous loops, raphide cells elongate with multiple or overlapping bundles, and laticifers non-anastomosing. The presence of a broad array of raphide types in these genera (Keating, 2004), and the *rbc*d and *mat*K gene consensus tree, suggests an affinity with the following tribes Areae and Colocasieae.

Tribe Areae now contains seven genera that extend from the Mediterranean region to India and Sri Lanka, Africa, southeast Asia into China, Malaysia, and northeastern Australia. They are: *Typhonium*, *Theriophonum*, *Biarum*, *Arum*, *Eminium*, *Dracunculus*, and *Helicodiceros*. The plants are tuberous and have similar anatomy that includes type 3 ground aerenchyma, type II vascular bundles, leaf venation with ascending secondary veins and brochidodromous loops, reticulate fine venation, non-anastomosing laticifers with transparent contents, and raphides occurring in elongated cells (Keating, 2004). A likely close relationship among these genera is supported by DNA sequence evidence.

Tribe Colocasieae occurs in Africa, south and east Asia, Malaysia, and northern Australia. The six genera are: *Ariopsis*, *Alocasia*, *Remusatia*, *Colocasia*, *Steudnera*, and *Protarum* (Seychelle Islands). Shared structural features include parallel and merging leaf tertiary veins, variable patterns of leaf aerenchyma, laticifers non-anastomosing or anastomosing, and biforines often present.

Genera of Colocasieae have been variously placed. They were regarded as a coherent grouping by Grayum (1990), except that he placed *Ariopsis* in a different subfamily. Bogner and Nicolson (1991) placed the six genera among four separate tribes. The cpDNA tree as well as anatomical evidence yield no rationale suggesting separate tribal status for any of these genera, except that half possess anastomosing laticifers and half non-anastomosing, a circumstance not considered to influence tribal affinities in previous classifications. The *rbc*d and *mat*K consensus tree is equivocal, placing *Alocasia* on a separate branch. If these genera otherwise prove to constitute a natural group, an in-

vestigation regarding evolution and relationship of laticifer types among the genera should be undertaken.

In the recent past, an accelerating tempo of additional data is yielding closer approximations to the truth. Family-wide data surveys by a number of workers have been instrumental in sharpening our understanding of this complex and ancient family. As reviewed by Mayo et al. (1997), Croat (1998), and Keating (2002, 2003), these results have clarified our understanding of relationships within the family, and the family's place among the monocots. The Araceae are ready for developmental surveys that should produce major advances in our understanding when integrated with DNA sequence results from all available genomes and with data on phenotypic structure and secondary chemistry.

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APPENDIX 1. Revised classification of the genera of Araceae.

Family Araceae Juss., 1789

Subfamily Gymnostachydoideae Bogner & Nicolson, 1991
Gymnostachys R. E. Br.
Subfamily Orontioideae Mayo, Bogner & P. C. Boyce, 1997
Tribe Orontieae R. Br., 1827
Orontium L.
Tribe Symplocarpeae Engl., 1876
Lysichiton Schott
Symplocarpus Salisb.
Subfamily Pothoideae Engl., 1876
Tribe Pothoeae Bartl., 1830
Pothos L.
*Pedicellarum** M. Hotta
*Pothoidium** Schott
Anthurium Schott
Tribe Monstereae Engl., 1876
Holochlamys Engl.
Spathiphyllum Schott
Rhodospatha Poepp.
Stenospermation Schott
Scindapsus Schott
Rhaphidophora Hassk.
Anadendrum Schott
Monstera Adans.
*Alloschemone** Schott
Epipremnum Schott
Amydrium Schott
*Heteropsis** Kunth
Subfamily Lasioideae Engl., 1876
Cyrtosperma Griff.
*Lasimorpha** Schott
*Podolasia** N. E. Br.
Lasia Lour.
Anaphyllum Schott
Urospatha Schott
Anaphyllopsis A. Hay
*Pycnospatha** Thorel.
Dracontium L.
Dracontioides Engl.
Subfamily Calloideae Endl., 1837
Calla L.
Subfamily Philodendroideae Engl., 1876
Tribe Philodendreae Schott, 1856
Montrichardia Crüger
Anubias Schott
Furtadoa M. Hotta
Philodendron Schott
Homalomena Schott
Tribe Zantedeschieae Engl., 1887
Zantedeschia Spreng.
Callopsis Engl.
Tribe Stylochaetoneae Schott, 1856
Stylochaeton Lepr.
Tribe Zamioculcadeae Schott ex Engl., 1876
Gonatopus Hook.f.
Zamioculcas Schott
Tribe Aglaonemateae Engl., 1876
Vephthytis Schott
Anchomanes Schott
*Pseudohydrosme** Engl.
Aglaonema Schott
Aglaodorum Schott
Tribe Culcasieae Engl., 1887
Culcasia P. Beauv.
Cercestis Schott
Tribe Spathicarpeae Schott, 1856
Bognera Mayo & Nicolson
Dieffenbachia Schott
Spathantheum Schott
Gorgonidium Schott
Synandrospadix Engl.
*Gearum** N. E. Br.
Spathicarpa Hook.
Asterostigma Fisch. & C. A. Mey.
*Mangonia** Schott
Taccarum Brongn.
Subfamily Schismatoglottidoideae R. C. Keating, subfam. nov.
Tribe Cryptocoryneae Blume, 1836
Cryptocoryne Fisch.
Lagenandra Dalz.
Tribe Schismatoglottideae Nakai, 1943
Phymatarum M. Hotta
Schismatoglottis Zoll. & Moritzi
Aridarum Ridl.
Piptospatha N. E. Br.
*Bucephalandra** Schott
Subfamily Lemnoideae Bab., 1843
*Spirodela** Schleid.
*Landoltia** D. H. Les & D. J. Crawford
Lemna L.
*Wolffia** Hork.
*Wolffiella** (Hegelm.) Hegelm.
Subfamily Aroideae Arn., 1832
Tribe Thomsonieae Blume, 1837

Amorphophallus Bl.
Pseudodracontium N. E. Br.
Tribe Caladieae Schott, 1832
Hapaline Schott
Syngonium Schott
Xanthosoma Schott
Chlorospatha Engl.
Ulearum Engl.
*Filarum** Nicolson
Zomicarpella Post & Kuntze
Caladium Vent.
*Scaphispatha** Brongn.
*Jasarum** G. S. Bunting
Zomicarpa Schott.
Tribe Arisareae Dumort., 1827
Ambrosina F. Bassi
Arisarum Mill.
Tribe Peltandreae Engl., 1876
Peltandra Raf.
Typhonodorum Schott
Colletogyne Buchet
Carlephyton Jum.
Arophyton Jum.
Tribe Pistieae Rich, 1831
Pistia L.
Tribe Arisaemateae Nakai, 1943
Arisaema Mart.
Pinellia Ten.
Tribe Areae R. Br., 1828
Typhonium Blume
Theriophonum Blume
Biarum Schott
Arum L.
*Eminium** (Blume) Schott
*Dracunculus** Mill.
Helicodiceros Schott
Tribe Colocasieae (Schott) Brongn., 1843
Ariopsis Rojas
Alocasia (Schott) G. Don
Remusatia Schott
Colocasia Schott
Steudnera K. Koch
*Protarum** Engl.

*Genera not included in the cpDNA survey of French et al. (1995).

APPENDIX 2. Definitions of character state typology.

Detailed descriptions of vegetative anatomical characters can be found in Keating (2002). For the character states discussed here, the following typology applies. Other terms not further defined below are used in the usual sense of contemporary anatomy texts.

Collenchyma. Type C: a strand that forms a cap over or near the phloem of a vascular bundle. **Type B**: a perimeter band of collenchyma that ensheaths the abaxial side of a midrib or petiole. **Type Bi**: collenchyma bands that are interrupted infrequently. **Type Sv**: collenchyma strands arranged around the perimeter of a midrib or petiole, and aligned on the same radius as the outer vascular bundles. They are either circular or not close enough to vascular bundles to be considered caps. **Type Sb**: collenchyma strands near an organ perimeter that are arranged between vascular bundles, or not in relation to vascular bundles.

Vascular bundles. Type I: broad bundles with semicircular strands of xylem and phloem separated by a wide straight boundary. Several files of metaxylem cells are present. **Type II**: a narrower bundle with shorter boundary between xylem and phloem. Only a few metaxylem cells are present. **Type III**: a bundle dominated by a single large, persistent, protoxylem lacuna opposite a narrow phloem strand.

Aerenchyma cavities. Type 3: numerous large cavities separated from each other by uniseriate partitions. **Type 4**: a few large cavities present separated by bi- or multiseriate partitions.

Raphides. Biforines are spindle-shaped cells with lignified walls, bearing a single raphide bundle. Cell ends usually bear thin-walled papillae. **Biforine-like cells** have thinner, non-lignified walls and undifferentiated cell ends.

APPENDIX 3. Description of subfamily
Schismatoglottidoideae R. C. Keating, subfam. nov.

Haec subfamilia a ceteris subfamiliis Aracearum habitu plerumque aquatico amphibiove, interdum terrestri, caule rhizomatoso plerumque epigaeo decumbenteve, vagini petiolari saepe ligula apicali munita, laminae foliaris vena marginali solitaria, spathae tubo connato persistente spadicis floribus sterilibus vel axe nudo flores pistillatos staminosque separante, antherarum poro apicali dehiscentium thecis truncatis cornutisve atque pollinis granis inaperaturatis plerumque psilatis distinguitur.

Plants occasionally terrestrial, mostly aquatic or amphibious, stems rhizomatous, mostly epigeal or decumbent, leaves several to numerous, petiole sheath often with apical ligule, blades elliptic, linear or sagittate, primary lateral veins pinnate usually with single marginal vein, higher-order veins parallel pinnate or transverse reticulate. Laticifers non-anastomosing, in all organs or absent from leaves. Inflorescence solitary, rarely two per sympodium, spathe tube connate, persistent, spadix with unisexual flowers with perigone absent, sterile flowers or naked axis separating female and male flowers. Stamens 1 to 2 (to 4), free or fused, thecae truncate or horned, dehiscent with apical pore. Pollen inaperaturate, mostly psilate. Ovary 1-locular, ovules 1 to many. Stigma sessile, discoid or capitate. Fruit a berry or syncarp. Seeds ellipsoid, embryo axile, straight, elongate. Endosperm present, often copious.

SYSTEMATIC OCCURRENCE OF RAPHIDE CRYSTALS IN ARACEAE[1]

Richard C. Keating[2]

Abstract

The presence of idioblastic cells bearing calcium oxalate raphide crystals is a defining character for Araceae. This light microscopical survey of vegetative organs, mostly leaf and petiole tissues, of 104 out of 106 recognized genera of the family, plus *Acorus*, demonstrated the presence of several distinctive raphide crystal types and the sometimes specialized cells that bear them. Cell types may be unmodified with respect to neighboring cell shapes, or may be idioblastic and become wide, elongated, tubular, articulated, spindle-shaped, or biforine-shaped. Crystal bundles may be simple, compound, or oblique-overlapping. This variation is posted against a new classification of the family. Although each of the nine subfamilies has a unique collection of types, trends of specialization are obscure. Biforines are found only among the unisexual-flowered genera.

Key words: Anatomy, Araceae, calcium oxalate, crystals, idioblast, raphide.

Raphide crystals are most commonly encountered among monocotyledonous families of flowering plants (Dahlgren & Clifford, 1982). For the Araceae, raphide presence is a defining character whose absence has been useful in, for instance, excluding the Acoraceae from the family (Grayum, 1987). However, it is also interesting to note that raphides are not reported to occur within Alismatiflorae (Dahlgren & Clifford, 1982; Tomlinson, 1982). The included families are now believed to be the nearest neighbors of aroids in a recent ordinal classification (Angiosperm Phylogeny Group (APG), 1998). As presently constituted, the Araceae include most of the 103 genera listed in Mayo et al. (1997) plus the five genera of Lemnaceae, yielding a current total of 106 genera (Table 1). The lemnoid genera are clearly embedded within the family based on DNA sequences (see Keating, 2002, 2003, 2004 this volume).

This investigation of araceous raphide crystals is aimed at enumerating the variety of types of raphide-bearing cells and crystal bundles as they occur in vegetative structures in the family. Secondly, the resulting typology was plotted against a contemporary classification (Keating, 2004) in order to assess potential evolutionary trends or systematic concordance.

Knowledge of this idioblastic cell type in the Araceae began with the description of biforines by Turpin (1836). Since then, various systematic accounts of raphides have been published including those of Buscalioni (1895–1896: 4 genera), Solereder and Meyer (1928: 16 genera), and Genua and Hillson (1985: 14 genera). The development and chemistry of raphides has been subject to a few detailed studies, and the subject has been reviewed by Franceschi and Horner (1980). In each case raphides are found to be monoclinic crystals of calcium oxalate monohydrate (whewellite). They appear to occur universally as bundles of needle-shaped crystals within vacuolar crystal chambers of idioblastic cells. Sakai et al. (1972) and Cody and Horner (1983) described deep grooves on raphide surfaces of *Colocasia*, *Alocasia*, and *Xanthosoma*. In addition, such crystals may also have backward-oriented surface barbs capable of increasing damage to the mouths of grazing animals.

Materials and Methods

Samples of vegetative material representing 106 genera were prepared for a general light microscopic (LM) histological survey. Only *Bognera* and *Landoltia* (Lemnoideae) are missing. About 380 species, mostly liquid-preserved, were examined for general histology of leaf lamina, petiole, stem, and root, and are listed in detail in Keating (2002). Therefore, the specimens examined list (see Appendix 1) here is only representative. For some specimens, microtechnique was accomplished using conventional paraffin techniques (Ruzin, 1999; Berlyn & Miksche, 1976). For others, hand sections were produced that were stained in cresyl violet

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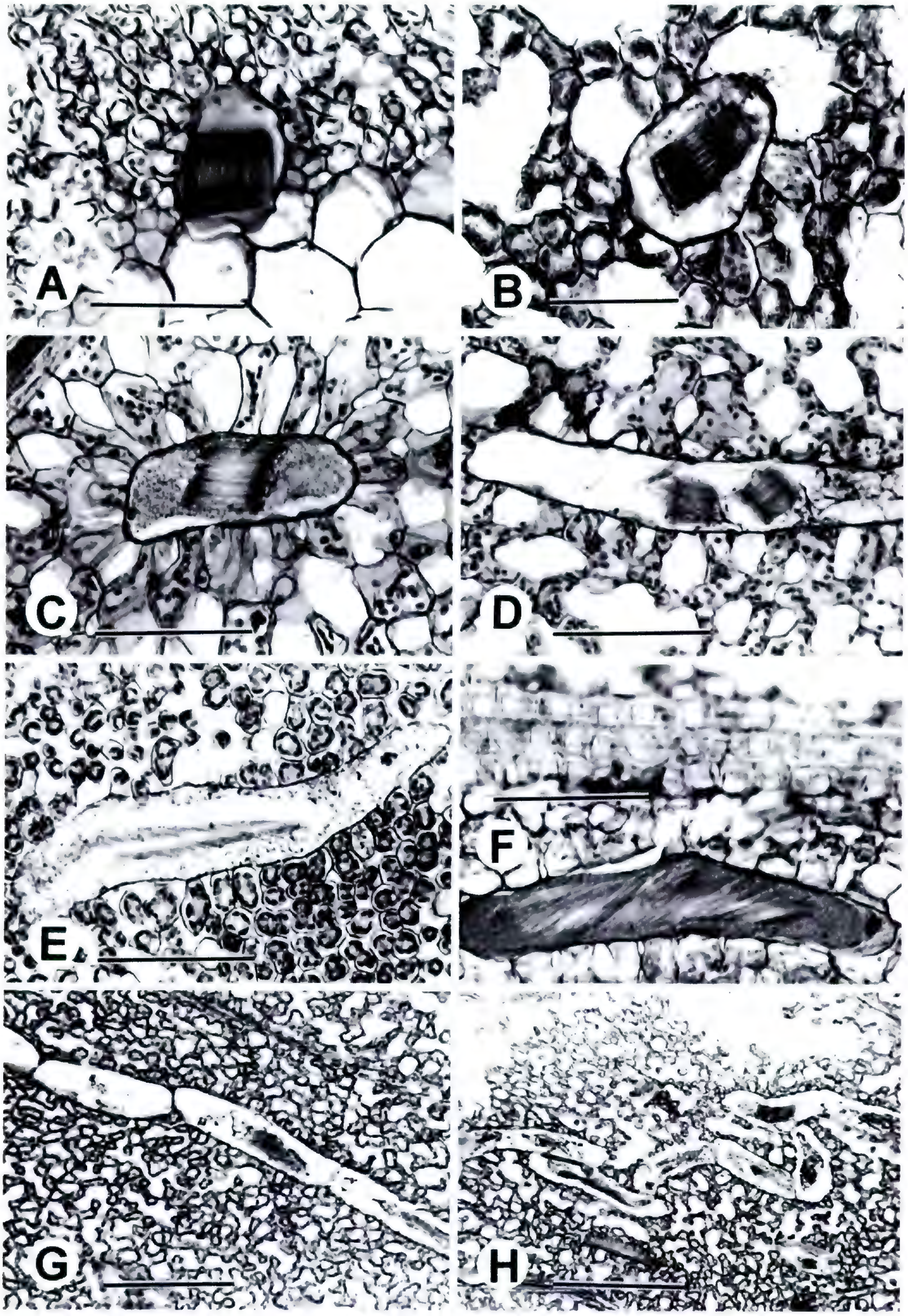

Figure 1. Paradermal leaf sections showing raphide crystal-bearing cells. —A. *Monstera acuminata.* Simple raphide cell containing wide crystal packet. —B. *Lysichiton camptschatcensis.* Simple raphide cell suspended within spongy mesophyll. —C. *Anubias barteri.* Elongated cell with single packet. —D. *Spathantheum orbignyanum.* Simple raphide tube with two short crystal packets. —E. *Anthurium polyschistum.* Tubular cell containing oblique overlapping crystal packet. —F. *Pedicellarum paiei.* Elongate raphide cell containing oblique overlapping, helical raphide packet. Above, note rows of rhombohedral crystals, rare in the family, along the vascular bundle. G, H. *Asterstigma riedeliana.*—G. Straight articulated raphide tube. —H. Sinuous articulated raphide tube. Scale lines: A, C–F = 200 μm; B = 100 μm; G, H = 500 μm.

acetate and wet-mounted in calcium chloride solution. With its high refractive index, calcium chloride is an excellent mountant (Herr, 1992; Keating, 1996) for observing general histology. However, with time, calcium oxalate crystals will erode in its presence. Because of the focus here on crystals, hand sections were also wet-mounted in glycerine, a mountant in which crystals appear to be archival. However, use of glycerine or other alcohols precludes permanent staining of cell walls or contents. Initial orientation to observing calcium oxalate crystals is improved by using polarized light. This type of crystal can also be detected and seen clearly with bright field LM. One stops down the substage diaphragm to a point where diffracted light from the crystals provides sufficient contrast for detection.

The data are arrayed in Table 1 according to a new family classification sequence (Keating, 2004) that was influenced by structural data and the available DNA sequence studies (French et al., 1995: cpDNA restriction sites; Cabrera et al., in prep.: *rbc*d and *mat*K genes; and Rothwell et al., 2004: chloroplast *trn*L–*trn*F intergeneric spacers). The subfamilial and tribal names recognized in the list are adopted as discussed in Keating (2004). Twenty-one genera not included in the cpDNA survey (French et al., 1995) were easily inserted here on the basis of placement by Mayo et al. (1997) and by the general anatomical concordance.

Observations

A surprising variety of crystal-bearing cells and crystal bundle configurations was encountered as described and illustrated below. It is possible to consider the cell characteristics and the crystal-bundle characteristics independently. Also, it was discovered early that the greatest diversity of types occurs in the lamina, with progressively less complexity occurring in ground tissue of the petiole, stem, and root. Roots usually have only the unmodified (U) type. Therefore, this survey emphasizes the lamina and, in so doing, I believe no unique types are left unaccounted for. Examination of the petiole may add the U type if it is not encountered in the lamina. Almost universally, some raphides are present in all organs examined, even if rarely encountered.

Within raphide-bearing cells, cytological structure and staining behavior suggest the existence of wide variation in the amount and type of compounds that are included within or surrounding the crystal chamber. Often these other contents are deeply staining or nearly opaque, obscuring the crystals themselves. Most frequently, crystals are not obscured by other materials. This chemistry was not further investigated in this study.

Crystal and cell typology

Unmodified (U) cells are irregularly shaped, and usually considerable cytoplasmic space coexists with the crystal bundles (Fig. 1A, B). U cells are widespread in the family, not always common, and they appear to be missing in some genera. In roots and stems, which have larger parenchymatous tissue cells, these isodiametric or irregular crystal-bearing cells often vary little in shape and size from neighboring parenchymatous tissue, the only idioblastic feature being the inclusion of crystalline contents. In leaves, U cells are less common than the more specialized types described below. Within mesophyll tissue they are larger than typical mesophyll parenchyma cells but remain thin-walled and contain one raphide bundle. Crystal bundle length is 2–3× that of bundle width.

Styloids (S), also called pseudoraphides by Dahlgren and Clifford (1982), are monoclinic crystals of raphide length, but are broader. They occur individually within cells or may be aggregated within bundles as coarse raphides. The S type occurs rarely (*Anadendron, Gonatopus, Zamioculcas, Amorphophallus*) and is never common.

Wide cells (W) often approach spheroidal in shape and usually contain a broad raphide bundle where its width approaches or exceeds bundle length (Fig. 1A). The cells often are similar to type U but are defined by a combination of cell shape and bundle width. They appear more frequent in genera appearing early in the classification (Table 1) and are quite uncommon in the subfamily Aroideae.

Elongated cells (E) are about 3× the length of usual crystal bundles (Fig. 1C), and they may include 2 or more bundles, coded as (2+) (Fig. 1D). E cells may contain oblique-overlapping bundles (Ov), which may occupy most or all of the length of the cell (Fig. 1E, F). Ov crystals may appear to be helical in orientation or the crystals are obliquely stacked in only one plane. Elongated cells are mostly concentrated in subfamilies branching at nodes earlier than the Aroideae. This cell type, as well as the preceding raphide types, was referred to as "non-defensive raphide idioblasts" by Sunell and Healey (1985).

Tubular cells (T) are 4× or greater in length than the included crystal bundle (Fig. 1D). They are most common earlier than the Aroideae but also occur in that subfamily. While not as common as

Table 1. Revised classification of Araceae[1] showing raphide cell and crystal types encountered in each genus.

Family, subfamily, or tribe	Genus	Raphide type[2]
ACORACEAE	*Acorus*	(−)
ARACEAE		
Gymnostachydoideae	*Gymnostachys*	U, E: 2+
Orontioideae		
Orontieae	*Orontium*	U, E: 2+
Symplocarpeae	*Lysichiton*	U, W, E
	Symplocarpus	U, W, Sb
Pothoideae		
Pothoeae	*Pothos*	U, ET: Ov
	Pedicellarum	U,T: Ov
	Pothoidium	U, E: Ov
	Anthurium	U, E: Ov
Monstereae	*Holochlamys*	U, E: Ov
	Spathiphyllum	U, W, E: Ov
	Rhodospatha	U, W, E: Ov 2+
	Stenospermation	U, E: Ov 2+
	Scindapsus	U, E: Ov
	Rhaphidophora	E: Ov
	Anadendrum	(S), U, E: Ov
	Monstera	U, E: Ov
	Alloschemone	U, E: Ov
	Epipremnum	U, W, E: Ov
	Amydrium	E: Ov
	Heteropsis	U, T: Ov 2+
Lasioideae	*Crytosperma*	U, W, E: Ov 2+, Sb
	Lasimorpha	U, W, E: Ov, Sb
	Podolasia	U, W, E: 2
	Lasia	U, ET: 2+
	Anaphyllum	U, E
	Urospatha	U, W, E: Ov 1–2+
	Anaphyllopsis	E: OV
	Pycnospatha	(S), U, W, E: Ov 2+
	Dracontium	U, W, ET: 2+
	Dracontioides	U, E: 2
Calloideae	*Calla*	U, Sb
Philodendroideae		
Philodendreae	*Montrichardia*	U, Sb
	Anubias	U, W, B
	Furtadoa	U, W
	Philodendron	U, E: Ov, Sb, B
	Homalomena	U, WE: 2+, B
Zantedeschieae	*Zantedeschia*	U, E: Ov, Sb, (B)
	Callopsis	U
Stylochaetoneae	*Stylochaeton*	U, W, B
Zamioculcadieae	*Gonatopus*	U, W, E: Ov
	Zamioculcas	U, W: 2+
Aglaonemateae	*Nephthytis*	U, E: 2+, B
	Anchomanes	U, E: Ov, B
	Pseudohydrosme	U, W, E: Ov, B
	Aglaonema	U, E, B
	Aglaodorum	B
Culcasieae	*Culcasia*	U, WE: Ov 2+, Sb, B
	Cercestis	U, ET: 2+, Sb
Spathicarpieae	*Bognera*	
	Dieffenbachia	UE: 2+, B
	Spathantheum	U, W, ET: 2+
	Gorgonidium	U, E: 2+
	Synandrospadix	U, W: 2+

Table 1. Continued.

Family, subfamily, or tribe	Genus	Raphide type[2]
	Gearum	W, E: 2+, B
	Spathicarpa	U, W, E: 2+
	Asterostigma	U, Ta
	Mangonia	U, W, E: Ov 2+
	Taccarum	U, W, E: 2+, Ta, (Sb)
Schismatoglottidoideae		
Cryptocoryneae	*Cryptocornye*	U, W, E: Ov 2+, Sb
	Lagenandra	U, WE: Ov
Schismatoglottideae	*Phymatarum*	U, W, E: Ov
	Schismatoglottis	U, W, B
	Aridarum	U, (B)
	Piptospatha	U, E, B
	Bucephalandra	U, W, Sb
Lemnoideae	*Spirodela*	U, E
	Landoltia	
	Lemna	U, E: Ov, Ta
	Wolffia	E?
	Wolffiella	E?
Aroideae		
Thomsonieae	*Amorphophallus*	S, U, E: 2+
	Pseudodracontium	U, W, E: Ov
Caladieae	*Hapaline*	U, W, B
	Syngonium	U, W, B
	Xanthosoma	U, W, (E), B
	Chlorospatha	U, Sb
	Ulearum	U, ET: Ov
	Filarum	U, E: 2+
	Zomicarpella	U, ET: Ov 2+, B
	Caladium	U, B
	Scaphispatha	U, B
	Jasarum	U
	Zomicarpa	U, E: 2+, B
Arisareae	*Ambrosina*	W, E: 2+
	Arisarum	U, E
Peltandreae	*Peltandra*	U, W, B
	Typhonodorum	U, B
	Colletogyne	U, B
	Carlephyton	U, W, Sb, B
	Arophyton	U, Sb, B
Pisteae	*Pistia*	U, Sb, B
Arisaemateae	*Arisaema*	W, T: Ov 2+
	Pinellia	U, E: 2+
Areae	*Typhonium*	U, W, ET: Ov 2+
	Theriophonum	U, E: Ov 2+
	Biarum	U, ET: 2+, Ta
	Arum	U, W
	Eminium	U, E: Ov 2+
	Dracunculus	U, W, E: 2+
	Helicodiceros	U, ET: Ov
Colocasieae	*Ariopsis*	U, E: 2+, B
	Alocasia	U, W, ET: 2+, Sb, B
	Remusatia	U, WE: 2
	Colocasia	U, B
	Steudnera	U, W, E: 2+
	Protarum	U, B

[1] Classification based on Keating (2004).

[2] S = styloid; U = unmodified cell with single raphide bundle; W = wide cell usually containing wide raphide bundle; E = elongated cell; T = tubular cell; Ta = articulated tube; Sb = thin-walled spindle-shaped cell; B = biforine; ( ) = occasional; 2+ = two or more bundles per cell; Ov = oblique overlapping, usually elongate crystal bundle.

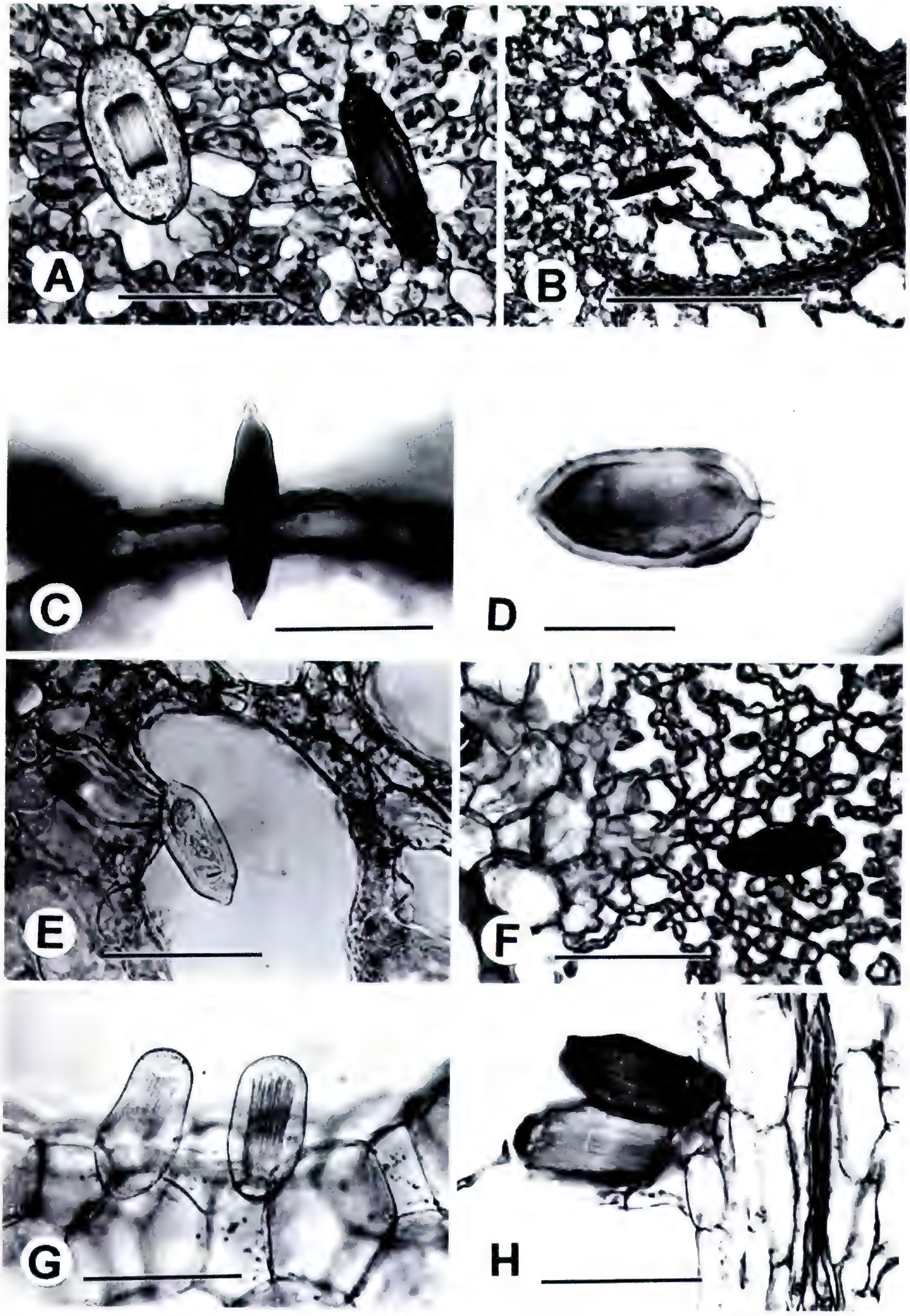

Figure 2. Raphide cells in leaf and petiole sections. —A. *Anubias barteri.* Leaf paradermal section, spongy mesophyll, showing elongated raphide cells. —B. *Syngonium angustatum.* Leaf paradermal section showing three biforine cells arranged randomly in spongy mesophyll. —C. *Pistia stratiotes.* Leaf base transverse section showing biforine raphide suspended across aerenchyma partition. —D, E. *Philodendron bipinnatifidum.*—D. Petiole center section showing detached biforine cell. Note very thick wall and terminal orifices through which raphide crystals can extrude. —E. Midrib transverse section showing thick-walled biforine suspended by oblique attachment to walls of aerenchyma

elongated cells, both types are equally likely to possess multiple bundles or oblique overlapping bundles.

Articulated tubes (Ta) are the rarest type found in the family, being only in *Asterostigma* and *Taccarum* (Spathicarpieae), *Lemna* (Lemnoideae), and *Biarum* (Areae). Each cell of a chain contains one crystal bundle. They are found as straight lines of cells (Fig. 1G) or taking a highly sinuous path (Fig. 1H), in either case coursing randomly through the mesophyll as seen in clearings or paradermal sections. In the case of *Lemna*, articulated cell chains are shorter than found in larger-leaved genera.

Spindle-shaped (Sb) cells are thin-walled, may be straight-sided, or have side-walls tapering toward both ends (Fig. 2A, G, H). Ends are usually rounded. Sb cells may be embedded within various types of parenchyma (Fig. 2F). Frequently they are found within aerenchyma where they may take several orientations: (a) parallel to and embedded within an air-space partition, (b) orthogonal to air-space partitions with the ends pointing into adjacent air cavities, or (c) they may be attached by one end with the other entirely suspended within an air cavity (Fig. 2G, H). Sb cells are most frequently found above the lasioids but are also found within *Symplocarpus*, *Cyrtosperma*, and *Calla*. They grade into:

Biforines (B). These cells are the same basic shape as the Sb cells but differ in having lignified cell walls, as described by Turpin (1836). They are called "defensive raphide cells" by Sunell and Healey (1985). These cell walls reach their thickest in *Philodendron* subg. *Meconostigma*. The cell ends are usually, but not always, modified to include thin-walled papillae (Fig. 2C, D) through which raphide crystals are rapidly extruded when the side wall is deformed (see Middendorf, 1983; Sunell & Healey, 1985). As with Sb cells, biforines may be oriented across aerenchyma partitions (Fig. 2B, C), or attached by one end and suspended within an air cavity (Fig. 2E). No biforines are found in subfamilies appearing at lower nodes than the Philodendroideae in Table 1, that is, none are present within the bisexual or hermaphroditic genera. They reach their best development in the Philodendroideae where they are well represented in all six tribes.

Discussion

A general perusal of anatomical literature suggests that raphide (and general oxalate crystal) diversity in Araceae is exceeded nowhere else in the plant kingdom. But discerning its meaning and trends is another matter. No correlation matrix was meaningful using this data because of some inherent difficulties. First, although the typology listed in Table 1 can be consistently applied for purposes of recording presence of character states, the typology may be subject to some variation. Second, the depth of sampling within genera is quite variable. Third, attempts to make tables where states are plotted against tribes produced very little visible systematically interesting variation. Fourth, the degree to which some cell and crystal types may be precursors to other types, either ontogenetically or phylogenetically, is unknown. For example, the two crystal cells appearing in Figure 2A may represent developmental stages. Fully expanded tissues were sampled whenever possible, but crystalliferous cells may differentiate at different rates.

When plotting the occurrence of the crystal types versus subfamilies (Table 2), it is difficult to discern a marked pattern however useful these types may be for generic diagnosis, singly or in combination. The U type remains common in all groups and seems to be the basic type in the family. The W type is widespread but never dominant. It appears to be least common in the Aroideae. Elongate (E) cells seem somewhat more common in the less specialized genera. Tubular (T) cells are widespread but not common. No trend is discernable. Also, the 2+ crystal condition that especially marks lasioids is widespread and shows no real trend. Oblique-overlapping (Ov) crystals are markedly common in the Pothoideae, but remain present in unisexual subfamilies. They may be considered an early specialization that is retained. Articulated tubes (Ta) are rare and found in the Philodendroideae (*Asterostigma* and *Taccarum*) as well as in *Biarum* of the Aroideae. It seems likely that crystal cell articulation is independently developed in the two subfamilies, and its selective value is unknown.

The thin-walled spindle-shaped cells (Sb) occur early in the family and are possibly derived from the U type where less cell wall expansion encloses

←

partition. —F. *Carlephyton glaucophyllum*. Leaf paradermal section with spindle-shaped cell in mesophyll tissue. —G. *Alocasia cucullata*. Petiole transverse section showing aerenchyma partition with two spindle-shaped cells attached by one end. —H. *Typhonodorum lindleyanum*. Paradermal section showing two spindle-shaped cells suspended into aerenchyma cavity. Scale lines: A, C, E–H = 200 μm; B = 300 μm; D = 100 μm.

Table 2. Occurrence of raphide cell and crystal types in subfamilies of Araceae.[1]

Subfamily	Raphide cell or crystal type[2]									
	U	W	E	2+	Ov	T	Ta	Sb	B	S
Gymnostachydoideae	1/1	(−)	1/1	1/1	(−)	(−)	(−)	(−)	(−)	(−)
Orontioideae	3/3	2/3	2/3	1/3	(−)	(−)	(−)	1/3	(−)	(−)
Pothoideae	14/16	3/16	13/16	3/16	16/16	3/16	(−)	(−)	(−)	1/16
Lasioideae	9/10	6/10	9/10	7/10	5/10	1/10	(−)	2/10	(−)	(−)
Calloideae	1/1	(−)	(−)	(−)	(−)	(−)	(−)	1/1	(−)	(−)
Philodendroideae	24/26	12/26	16/26	12/26	6/26	2/26	1/26	6/26	13/26	(−)
Schismatoglottidoideae	9/9	5/9	4/9	1/9	3/9	(−)	(−)	2/9	2/9	(−)
Lemnoideae	2/4	(−)	2/4	(−)	1/4	(−)	1/4	(−)	(−)	(−)
Aroideae	34/38	11/38	20/38	18/38	8/38	6/38	1/38	5/38	17/38	1/38

[1] Number of genera with character/number of genera in subfamily.
[2] Raphide cell and crystal type codes as given for Table 1.

a developing crystal bundle. Otherwise, no trend is visible. Biforine (B) cells are usually found in genera also containing Sb cells and are probably derived from this basic spindle shape by lignification of the walls and development of terminal papillae. They are not found in the first five subfamilies, but only in Philodendroideae and later listed genera. Therefore, the biforine form demonstrates the best apomorphic state transformation of any crystal cell type within the family. Types Sb and B tend to associate with aerenchyma having large air cavities. They are the only types that traverse partitions.

This is the first study to catalog the array of raphide cells and bundle configurations from a nearly complete generic sample of the family. It has been noted that frequency and distribution of raphides is not uniform within a genus or a species, often not even within a single organ (cf. Sunell & Healey, 1985). Therefore those aspects could not be rationally addressed in the limited sample available for a broad generic survey. The array and distribution of types observed here can provide a background for further study of many aspects of the biology of crystals in the family. Variations include those of texture, bundle size, shape, membrane system, and chemistry of inclusions within the membrane. Clearly, techniques in addition to LM will be needed in generating data regarding membranes, ontogeny, and chemistry.

Finally, I should note that rhomboids, druses, styloids, and crystal sand show some variations in form and distribution in the family and should be similarly investigated. The abundance of all calcium oxalate crystal types in the Araceae in various forms and configurations, and the ease with which numerous aroid genera can be grown, make the family an excellent choice for analytical work on crystal ontogeny, functioning, and evolution. In spite of hypotheses proferred regarding the function of calcium oxalate in plant tissues (cf. D'Arcy et al., 1996), our understanding of the evolution of crystals and their function remains largely speculative.

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APPENDIX 1. Specimens examined, one representative listed per genus.

Acorus calamus L., *Boufford 18710*, Missouri (MO); *Aglaodorum griffithii* Schott, *Bogner 1767*, cult. (M); *Aglaonema brevispathum* Engl., cult. (M); *Alloschemone occidentalis* (Poepp.) Engl. & Krause, *Sakuragui 1050*, Brazil, cult. (M); *Alocasia cucullata* (Lour.) G. Don, cult. MO 894185; *Ambrosina bassii* L., *Bogner 1521*, cult. (M); *Amorphophallus hildebrandtii* (Engl.) Engl. & Gehrm., *Bogner 168*, Madagascar, cult. (M); *Amorphophallus konjac* K. Koch, *Keating 2089*, cult. Illinois; *Amydrium medium* (Zoll. & Morr.) Nicolson, *Bogner 433*, Thailand, cult. (M); *Anadendrum microstachyum* (de Vries & Miq.) Backer & Alderw., *Bogner 1314*, cult. (M); *Anaphyllopsis americana* (Engl.) A. Hay, *A. Hay 2811*, French Guiana, cult. (M); *Anaphyllum beddomei* Engl., *Blasco s.n.*, S. India, cult. (M); *Anchomanes welwitschii* Rendle, *Croat 69773*, Gabon, cult. (MO); *Anthurium polyschistum* R. E. Schult. & Idrobo, cult. (M); *Anubias barteri* Schott var. *nana* (Engl.) Crusio, *Bogner 1301*, cult. (WAG); *Aridarum borneense* (M. Hotta) Bogner & A. Hay, *Bogner 1400*, Sarawak cult. (M); *Ariopsis peltata* J. Graham, *Bogner 1481*, cult. (M); *Arisaema tortuosum* Schott, cult. M; *Arisarum vulgare* Targ. Tozz., cult. (M); *Arophyton buchetii* Bogner, *Bogner 207*, Madagascar, cult. (M); *Arum italicum* Mill., cult. (M); *Asterostigma riedelianum* Kuntze, *Harley 18535*, Brazil: Bahia, cult. K.

Biarum tenuifolium (L.) Schott, S. Mayo, cult. (M); *Bucephalandra motleyana* Schott, *Bogner 1366*, cult. (M).

Caladium plowmanii Madison, *Plowman et al. 3979*, Ecuador, cult. (SEL); *Calla palustris* L., *Boufford 18801*, Ontario (MO); *Callopsis volkensii* Engl., *Bogner 218*, Tanzania, cult. (M); *Carlephyton glaucophyllum* Bogner, *Bogner 167*, Madagascar, cult. (M); *Cercestis congensis* Engl., *Bogner 353*, cult. (M); *Chlorospatha longipoda* (K. Krause) Madison, 23–76–122, cult. (SEL); *Colletogyne perrieri* Buchet, *Bogner 165*, Madagascar, cult. (M); *Colocasia fallax* Schott, *Bogner 1139*, India, cult. (M); *Cryptocoryne pontederiifolia* Schott, *Bogner 1093*, Sumatra, cult. (M); *Culcasia obliquifolia* Engl., *Bogner 654*, Gabon, cult. (M); *Cyrtosperma johnstonii* N. E. Br., *Bogner 2341*, cult. (M).

Dieffenbachia oerstedii Schott, *Croat 42645*, Honduras (MO); *Dracontioides desciscens* Engl., *Storr 075*, cult. (M); *Dracontium spruceanum* (Schott) G. Zhu, *Croat 34334*, Panama (MO); *Dracunculus canariensis* Kunth, *Bogner 1519*, Gran Canaria, cult. (M).

Eminium alberti Engl., *Wilson & Mewer 765*, cult. (K); *Epipremnum pinnatum* Engl., cult. (MO).

Filarum manserichense Nicolson, *Wurdack 2402*, Peru (K); *Furtadoa sumatrensis* M. Hotta, Bogor, cult. (M).

Gearum brasiliense N. E. Br., *Burchell 8598*, Brazil (K); *Gonatopus boivinii* (Decne.) Engl., cult. (M); *Gorgonidium mirabile* Schott, Bolivia, cult. (M); *Gymnostachys anceps* R. Br., *Rodd 2326*, Australia, cult. (M).

Hapaline brownii Hook.f., *Burtt & Woods 1771*, cult. (M); *Helicodiceros muscivorus* Engl., 1032/73, cult. (M); *Heteropsis spruceana* Schott, *Croat 33808*, Panama (MO); *Holochlamys beccarii* Engl., *Bogner 1269*, New Guinea, cult. (M); *Homalomena peltata* (Poepp.) Masters, *Croat 38285*, Canal Zone (M).

Jasarum steyermarkii Bunting, *Herkner & Jeschke s.n.*, Venezuela, cult. (M).

Lagenandra erosa DeWit, *Bogner 450*, Ceylon, cult. (M); *Lasia spinosa* f. *simplex* Thwaites, *Bogner 428*, Thailand, cult. (M); *Lasimorpha senegalensis* Schott, *Bogner 691*, West Africa, cult. (M); *Lemna minor* L., cult. (M); *Lysichiton camtschatcensis* Schott, cult. (M).

Mangonia tweediana Schott, *Bogner 2376*, Brazil, cult. M; *Monstera acuminata* C. Koch, *Croat 42933*, Nicaragua (MO); *Montrichardia arborescens* (L.) Schott, *Croat 38331*, Canal Zone (MO).

Nephthytis afzelii Schott, *Knecht 23/198*, Cote d'Ivoire, cult. (M).

Orontium aquaticum L., *Boufford 18027*, North Carolina (MO).

Pedicellarum paiei M. Hotta, *Paie 16354*, Sarawak, cult. (K); *Peltandra sagittifolia* (Michx.) Morong, *Boufford 18467*, Florida (MO); *Philodendron bipinnatifidum* Schott, cult. (SIUC); *Phymatarum borneense* M. Hotta, *Bogner 1476*, Sarawak, cult. (M); *Pinellia tripartita* Schott, 1977, *s.n.*, cult. (M); *Piptospatha elongata* N. E. Br., *Bogner 1478*, Sarawak, cult. (M); *Piptospatha lucens* (Bogner) Bogner & A. Hay [originally studied as *Hottarum lucens*], *Bogner 1439*, Sarawak, cult. (M); *Pistia stratiotes* L., cult. (MO); *Podolasia stipitata* N. E. Br., *Anderson 26757*, Sarawak (K); *Pothoidiuim lobbianum* Schott, *Bogner 1272*, cult. (M); *Pothos remotiflorus* Hook., *Jayasuriya & Dassanayake 1016*, Ceylon (K); *Protarum sechellarum* Engl., *Gardiner 110*, Seychelles (K); *Pseudodracontium siamense* Gagnep., Kew 414–35–41401, cult. (M); *Pseudohydrosme gabunensis* Engl., *Breteler s.n.*, Gabon, cult. (LL); *Pycnospatha arietina* Gagnep., *Bogner 395*, Thailand, cult. (M).

Remusatia vivipara (Roxb.) Schott & Endl., spirit collection (K); *Rhaphidophora africana* N. E. Br., *Bogner 602*, Gabon, cult. (M); *Rhodospatha wendlandii* Schott, *Croat 43792*, Mexico (MO).

Sauromatum guttatum Schott (= *Typhonium*), *Keating s.n.*, cult. Edwardsville, IL; *Scaphispatha gracilis* Brongn. ex Schott, *Bogner 1211*, Brazil, cult. (M); *Schismatoglottis calyptrata* (Roxb.) Zoll. & Moritzi, MO hort. accession 772049, cult. (MO); *Scindapsus scortechinii* Hook. f., *Koerper s.n.*, Borneo, cult. (M); *Spathantheum orbignyanum* Schott, *Rauh 26024*, Peru, cult. (M); *Spathicarpa sagittifolia* Schott, *Bogner 2335*, cult. (M); *Spathiphyllum friedrichsthalii* Schott, *Croat 38312*, Canal Zone (MO); *Spirodela polyrhiza* (L.) Schleid., cult. (M); *Stenospermation angustifolium* Hemsl., *Croat 35255*, Costa Rica (MO); *Steudnera colocasiifolia* C. Koch, cult. (M); *Stylochaeton crassispathus* Bogner, *Bogner 143*, Tanzania, cult. (M); *Symplocarpus foetidus* (L.) Nutt., *Keating 2275*, Illinois; *Synandrospadix vermitoxicus* (Griseb.) Engl., *Bogner 1480*, Bolivia, cult. (M); *Syngonium angustatum* Schott, *Croat 42559*, Honduras (MO).

Taccarum weddellianum Brongn. ex Schott, *Bogner 458*, cult. (M); *Theriophonum minutum* Engl., *Mooney 3963*, India (K); *Typhonium mirabile* (A. Hay) A. Hay [originally studied as *Lazarum mirabile*], *Bogner s.n.*, cult. (M); *Typhonium roxburghii* Schott, 401/75 cult. (M); *Typhonodorum lindleyanum* Schott, cult. (M).

Ulearum sagittatum Engl., *Jangoux et al. 85-058 21-30*, cult. (MO); *Urospatha grandis* Schott, *Croat 35764*, Costa Rica (MO).

Wolffia arrhiza (L.) Horkel ex Wimm., cult. (M); *Wolffiella welwitschii* (Hegelm.) Monod, *G. Eggers s.n.*, Venezuela, cult. (M).

Xanthosoma sagittifolium (L.) Schott, *Metcalfe s.n.*, Canal Zone (K).

Zamioculcas zamiifolia Engl., *Bogner 126*, Tanzania, cult. (M); *Zantedeschia albomaculata* (Hook. f.) Baill., cult. (MO); *Zomicarpa riedeliana* Schott, *Bogner 1213*, cult. (M); *Zomicarpella amazonica* Bogner, *Croat 71763*, Brazil, cult. (MO).

THE PHYLOGENY OF THE COCOEAE (ARECACEAE) WITH EMPHASIS ON *COCOS NUCIFERA*[1]

Bee F. Gunn[2]

ABSTRACT

The tribe Cocoeae contains economically important palms including *Cocos nucifera, Elaeis guineensis, Attalea speciosa,* and *Bactris gasipaes.* This study, based on the nuclear *prk* gene sequence, addresses the monophyly of the subtribes of Cocoeae, the closest relatives of *Cocos nucifera,* and biogeographical implications of its distribution. The Cocoeae are divided into the spiny and non-spiny taxa. Molecular data alone suggest that *Cocos nucifera* did not originate in the western Pacific; it may be the only extant member of its lineage. Several Cocoeae fossils from New Zealand and India were used as calibration points to estimate times of divergence of clades. A hypothesis for the origin of the Cocos clade based on the phylogeny was postulated. It is hypothesized that Cocoeae originated from South America, diversified and radiated eastward toward Africa, Madagascar, and India, and southward to Australia and New Zealand via the Antarctic corridor. The estimated divergence dates were corroborated with major tectonic events.

Key words: Arecaceae, Cocoeae, coconut, *Cocos, prk* gene.

Palms (Palmae or Arecaceae) have been important in the lives of people since early civilization. As Purseglove (1972: 417) noted, palms provide "a wider range of economic products and multiplicity of uses than any other useful plants; in economic importance they are second only to the Gramineae." With the early domestication of the coconut, palms played a vital role in the colonization of the Pacific by the Austronesians (Bellwood, 1975).

The palm family includes 189 genera and about 2600 species found mainly in the tropics or subtropics (Uhl & Dransfield, 1999), but sometimes in warm temperate regions. They are especially diverse in Malesia and Amazonia, but are poorly represented in Africa (Moore, 1973a; Uhl & Dransfield, 1987). Work on the phylogeny of angiosperms has confirmed the monophyly of the palm family and its position among the basal commelinids (APG, 1998; Soltis et al., 2000).

Moore (1973a) arranged palms into 15 unranked major groups based on the presumed order of specialization from a series of morphological characters. He recognized the cocosoid palms as a single group because of their distinctive bony endocarps with three pores, and he also recognized three subgroups within the cocosoids, the Bactris, Cocos, and Elaeis alliances. Uhl and Dransfield (1987) later recognized six subfamilies and 14 tribes in Arecaceae. Cocoeae were treated as a distinctive tribe consisting of 22 genera divided into five subtribes similar to Moore's cocosoid major group but including *Beccariophoenix.* The Calamoideae (100% bs) and Phytelephantoideae (97% bs) are monophyletic based on 18S molecular data, but the Coryphoideae, Ceroxyloideae, and Arecoideae are not (Asmussen et al., 2000; Hahn, 2002a); Nypoideae are monotypic. The Cococeae are one of the eight tribes of Arecoideae, and are divided into five subtribes, 20 genera, and 206 species (Table 1; cf. Uhl & Dransfield, 1987; Henderson et al., 1995).

Cocoeae contain several economically important plants, including *Cocos nucifera, Elaeis guineensis* (African oil palm), *Attalea speciosa* (babaçu palm), and *Bactris gasipaes* (peach palm). Despite their economic importance, the phylogenetic history of the tribe has not been studied, and we do not know the closest relative of the coconut.

Nevertheless, the monophyly of Cocoeae is not in doubt (Asmussen et al., 2000; Lewis & Doyle, 2001; Hahn, 2002a, b). A striking synapomorphy of the group is the presence of three or more "eyes" or germination pores on the hardened seed endo-

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Table 1. Taxonomic hierarchy of tribe Cocoeae, sensu Uhl and Dransfield (1987) and Henderson et al. (1995). Numbers of species are followed by the taxon's distribution (Henderson et al., 1995).

Subfamily: Arecoideae
Tribe: Cocoeae
Subtribe: Attaleinae Drude
Attalea Kunth (29, Neotropics)
Subtribe: Butiinae Saakov
Allagoptera Nees (4, South America)
Butia (Becc.) Becc. (7, South America)
Cocos L. (1, pantropical)
Jubaea Kunth (1, Chile)
Jubaeopsis Becc. (1, South Africa)
Lytocaryum Tol. (2, Brazil)
Parajubaea Burret (2, South America)
Polyandrococos Barb. Rodr. (1, Brazil)
Syagrus Mart. (930, South America)
Voanioala J. Dransf. (1, Madagascar)
Subtribe: Bactridinae
Acrocomia Mart. (2, Neotropics)
Aiphanes Willd. (22, Neotropics)
Astrocaryum G. Mey. (18, Neotropics)
Bactris Jacq. ex Scop. (73, South America)
Desmoncus Mart. (7, Neotropics)
Gastrococos Morales (1, Cuba)
Subtribe: Beccariophoenicinae J. Dransf. & Uhl
Beccariophoenix Jum. & H. Perrier (1, Madagascar)
Subtribe: Elaeidinae Hook. f.
Elaeis Jacq. (2, Africa, Neotropics)
Barcella Drude (1, South America)

carp. Other distinguishing features include a once-branched (rarely spicate) inflorescence, an inconspicuous prophyll, a prominent and often woody peduncular bract that splits abaxially with respect to the main axis of the palm, imbricate petals of pistillate flowers, and a triovulate gynoecium (Uhl & Dransfield, 1987).

Cocoeae are widely distributed in the Neotropics (15 genera, Henderson et al., 1995), and two genera are found in Madagascar (*Beccariophoenix* and *Voanioala*) and two in Africa (*Jubaeopsis* and *Elaeis*, the latter also found in South America), while *Cocos nucifera* is pantropical. Historically, at least 60 species were included in *Cocos* by Martius (1824), Beccari (1916), Barbosa Rodrigues (1903), and Glassman (1987); these are now placed in either *Syagrus* or *Butia*. *Cocos* and *Syagrus* share many similarities, but may be distinguished by the size of their flowers and their fruits. *Syagrus* has globose pistillate flowers, and the apices of the sepals and petals are valvate. In contrast, *Cocos* has globose-ovoid pistillate flowers, and the apices of the sepals and petals are rounded. The fruits of *Syagrus* are smaller and contain much less liquid endosperm than those of *Cocos nucifera*.

The fruit of Cocoeae is a modified drupe, as is common in palms. Its epicarp is composed of sclerenchyma, which contains raphides and secondary compounds such as tannin. The mesocarp consists mainly of parenchyma and is usually fleshy and nutritious, for example, *Syagrus romanzoffiana*. In Cocoeae, the parenchymatous mesocarp layer is highly developed, and in *Cocos* it is thick and fibrous and contributes to buoyancy. The fruit endocarp is usually sclerenchymatous and is presumed to protect the developing seed from predation, desiccation, or crushing (Essig, 1977). Maturation of the fruit occurs basipetally in the Cocoeae and Arecoideae (Uhl & Moore, 1971); this is due to a basal meristemic zone that continues to divide until the fruit reaches half its final length, with further increase in fruit size due to cell enlargement (Murray, 1973). Sclerification of the cells also occurs basipetally; thus, the stylar regions become hard and protective before the base of the ovary (Uhl & Moore, 1971).

The current phylogeny of the Cocoeae suggests hypotheses about the origin of *Cocos nucifera*, which may have reached its present distribution by water and/or human dispersal. Various authors have suggested an origin in the western Pacific (Harries, 1978), Asia or Polynesia (Beccari, 1963; Corner, 1966), Melanesia (Moore, 1973b), or the Neotropics (Guppy, 1906; Cook, 1910; Hahn, 2002b). Currently, it is accepted by most scientists that the coconut probably originated in the western Pacific (Harries, 1978; Gruezo & Harries, 1984).

Molecular studies in the Arecaceae are fairly limited. Although family-wide studies conducted by Asmussen et al. (2000) investigated relationships among 65 species, only three representatives of Cocoeae were sequenced from plastid genes, *rps* 16 intron and *trn*L-*trn*F. Baker et al. (2000) surveyed 22 genera, all from subfamily Calamoideae using nrDNA (ITS) and cpDNA (rps16). Hahn (2002a) conducted combined analyses of all available palm data (65 species) including *atp*B, *rbc*L, 18S nr DNA, and morphology. He reported incongruence between the morphological and all the molecular data sets and also general lack of resolution and support. However, he noted the monophyly of Cocoeae (86%) represented by two taxa, *Beccariophoenix* and *Elaeis*. Lewis and Doyle (2002) examined 54 palm species using nr *malate synthase* and *phosphoribulokinase* (*prk*) genes for the Areceae tribe; two Cocoeae taxa were included as outgroups. Hahn's (2002b) Arecoideae phylogenetic study sampled 51 representatives of the arecoid line and

included 16 genera of Cocoeae using plastid genes *atp*B, *rbc*L, and *trn*L-*trn*F. This present study is the first comprehensive molecular investigation based on the nuclear gene *prk* of all 20 extant genera in Cocoeae, and 34 taxa were sampled across all five subtribes.

The aims of this study are to test the monophyly of Cocoeae subtribes Bactridinae, Butiinae, and Elaeidinae, and to investigate the relationship of *Cocos nucifera* within the tribe. A generic-level phylogeny of Cocoeae is presented here, based on the nuclear gene *prk*. A well-documented assemblage of Cocoeae fossil pollen and fruits from Africa, Australia, Easter Island, France, Germany, India, New Zealand, and South America has been compiled: several of the fruits were used to calibrate the divergence times of the clades.

Materials and Methods

TAXA

Thirty-four taxa representing all 20 genera recognized for the five subtribes of Cocoeae were sampled from living collections (33 accessions) and one from a dried herbarium specimen of *Parajubaea torallyi* (see Appendix 1). The sequences for the two outgroups, *Reinhardtia gracilis* and *Roystonea regia*, as well as that of one ingroup, *Allagoptera arenaria*, were retrieved from GenBank. The outgroups were chosen from results of the phylogeny of the Arecaceae (Hahn, 2002a, 2002b) and of the Arecoideae (Lewis & Doyle, 2002). Multiple accessions of *Cocos nucifera*—two tall varieties and one dwarf variety—were sampled, as they represented two distinct domesticated forms of the coconut. Two accessions of *Aiphanes aculeata* were sequenced because *Aiphanes caryotifolia* is now synonymous with *Aiphanes aculeata* (Borchenius & Bernal, 1996). Clones of the 34 taxa sequenced were included in the MP analysis to verify that they were all paralogue 2 of the *prk* gene (Lewis & Doyle, 2002).

DNA EXTRACTION

Genomic DNA was extracted from fresh leaves, silica-dried material, or herbarium specimens using large-scale CTAB and cesium chloride purifications (modified from Doyle & Doyle, 1987) and miniprep protocols (Doyle & Doyle, 1987). Phosphoribulokinase is an enzyme unique to the photosynthetic carbon reduction cycle and catalyzes the irreversible ATP-dependent synthesis of ribulose-1, 5 bisphosphate. The coding sequence of the *prk* gene is interrupted by four introns (Lloyd et al., 1991). This low-copy nuclear gene has been found to be useful in molecular studies at species and generic levels (Lewis & Doyle, 2002). Sequences of about 700 bp from exons 4, 5 flanking the fourth intron were obtained.

PCR, CLONING, AND SEQUENCING

Double-stranded DNA was amplified using the polymerase chain reaction (PCR). A two-step amplification protocol with semi-nested primers (488f and 1167r from flowering plants (non-palms); and 717f and 969r from palms) was used. Primers for the *prk* nuclear gene were designed by Lewis and Doyle (2002). Määgic buffer (modified from Pääbo, 1990, with addition of DMSO) was used in the PCR cocktail. Two μl of the product from the first step PCR served as the template for the second step PCR (50 μl reactions) using the internal set of primers designed for palms (717f and 969r: Lewis & Doyle, 2001). Thermal cycling conditions were as follows: 94°C, 4 min., followed by 35 cycles at 94°C, 1 min., 53°C, 1 min., 72°C, 2 min., concluding with 72°C, 7 min. PCR products were resolved on a 1% agarose gel, then purified by spinning them through Qiaquik columns (Qiagen™). The eluted products were further gel purified and passed again through Qiaquik columns. Amplified fragments of *prk* were then cloned using pGEM-T easy vector systems (Promega Corp.), reamplified with M13R and M13F (Kobs, 1995) universal primers, then purified with Qiaquik columns and resolved again on 1% agarose gels. Purified products were cycle sequenced using Big Dye Terminator (Perkin Elmer) using T7 and SP6 primers (Promega Corp., 1996). For *Bactris*, *Jubaeopsis*, and one sample of *Cocos nucifera* the amplification primers 717f and 969r (Lewis & Doyle, 2002) were used. The sequences were generated on an ABI 377 automated sequencer at the University of Missouri–St. Louis. At least three clones per plate were picked from each taxon for sequencing. Both the forward and reverse strands had overlaps of at least 70%, although the *Desmoncus chinantlensis* sequence had less overlap (60%). Contigs were assembled using Sequencher™ 3.1 (Gene Codes Corporation, 1991–1998).

SEQUENCE ALIGNMENT

Preliminary global alignments were performed using CLUSTAL X, Ver.1.8, 1999 (Thompson et al., 1997) and realigned visually with SE-AL version 1.dl (Rambaut, 1996). Sequences of each clone, including some direct sequences, were used for each individual taxon in the phylogenetic analysis (Fig.

1). Sequences were deposited in GenBank (accessions AY601206–AY 601273).

Phylogenetic Analysis

Parsimony analyses of molecular data were conducted using PAUP* 4.0b10 (Swofford, 1999). Maximum parsimony analyses (MP) were performed with heuristic search options as follows: tree-bisection-reconstruction (TBR) branch swapping, gaps coded as missing. The first 20 and last 24 characters were excluded from the analysis because they were the primer sites. Also excluded was the poly-A and G region in the fourth intron (bp 370–385) because it could not be unambiguously aligned. All characters were unordered, equally weighted, and outgroups were specified. Internal support for the clades was assessed by bootstrapping, with 100 replicates with 1000 random taxon addition replicates and TBR swapping.

Maximum Likelihood (ML) analyses were carried out using PAUP* 4.0b10. MODELTEST 3.06 (Posada & Crandall, 1998) was used to obtain the substitution model that fits the data best. MODELTEST 3.06 uses PAUP* to calculate likelihood scores for 56 models of evolution and compares the different nested models. Settings from the model test were used in PAUP to generate the maximum-likelihood tree using the Hasegawa-Kishino-Yano (1985) or HKY+ G model, with base frequencies: A = 0.2948, C = 0.1990, G = 0.2256, T = 0.2806; transition/transversion ratio = 1.8755; and gamma distribution shape = 1.0177. ML searches used a heuristic search strategy with 100 random taxon additions, holding five trees per step, TBR (tree bisection reconstruction), and branch swapping. The ML analyses were performed with and without molecular clock constraints. Under the clock regime, the maximum likelihood analysis was stopped after the log likelihood value reached a maximum likelihood of 4052.0311 and remained unchanged for two hours afterward.

The likelihood ratio test based on the differences between the log-likelihood of the two models indicates that the molecular clock could be rejected (**$P < 0.01$, df = 38). In order to infer age of divergence of the clades (in ML tree, Fig. 2), a Non Parametric Rate Smoothing (NPRS) of the tree was applied using the r8s program (Sanderson, 2000). Four fossils were used to calibrate the internal nodes of the tree. The fossils (see Fig. 2) F1 (Wharekuri—32 my), F2 (Boulder Hill, NZ—42 my), F3 (Waihao beaked—31 my), and F4 (*Cocos intertrappeansis*, India—50 my) were used separately to calibrate the internal nodes. The long branches of *Reinhardtia*, *Roystonea*, and *Barcella* were pruned because the rapid change of substitution rates from the long to short branches affected the estimated ages of divergence. A penalized likelihood analysis was used, which finds an optimal smoothing parameter or autocorrection to ameliorate the effects of rapid changes on tree and pruning. The estimated rates of divergence based on the chronograms (not shown) are included in Table 2.

Bayesian inference of phylogeny is a statistical approach based on the likelihood function and the prior probability distribution of trees (Huelsenbeck et al., 2002). The MrBayes (Huelsenbeck, 2000) program uses the Metropolis-coupled Markov Chain Monte Carlo to sample the best trees from the distribution of the posterior probabilities. The same Nexus data file created in PAUP was used in MrBayes 2.01 to generate the tree with the posterior probability closest to 1. The MODELTEST 3.06 model parameters used for the ML analysis were also used in the Bayesian analysis. Two million rearrangements were run, and every 1000th tree was saved. The burn-in number of trees was 1600.

Results

The total length of the *prk* aligned sequence was 672 nucleotide substitution sites. The maximum pairwise distance between sequences was 16% among the taxa excluding the outgroup. Pairwise similarity of the clones within a species was 93%–99%. The PCR error was 0.03%.

The MP topology for Cocoeae with all the clones included (72 sequences) shows the monophyly of the cloned taxa (Fig. 1). In the strict consensus of 14,071 MP trees, tree length was 524, the consistency index (CI), excluding uninformative characters, was 0.733, rescaled consistency index (RC) was 0.668, and the retention index (RI) was 0.911. The division of Cocoeae (excepting *Barcella*) into two main clades (Fig. 1), the non-spiny (94% bootstrap support (bs)) and spiny (98% bs) species, is fairly robust in this topology. *Barcella odora* is basal in Cocoeae (55%), with the clade forming the rest of the tribe having 78% bootstrap support. The non-spiny group includes a large clade (94% bs), plus *Beccariophoenix madagascariensis* and *Voaniaola gerardii* in a basal position (57%). Within the large non-spiny clade are the Cocos and Attalea alliances with *Jubaeopsis caffra* unresolved. The Cocos alliance itself (53% support) is composed of *Cocos nucifera*, (*Allagoptera leucocalyx* + *Polyandrococos caudescens*), (*Butia capitata*, *eriospatha* + *Jubaea chilensis*), (*Syagrus amara* + *S. smithii*, 100% bs) with *Parajubaea torallyi* unplaced. *Butia*

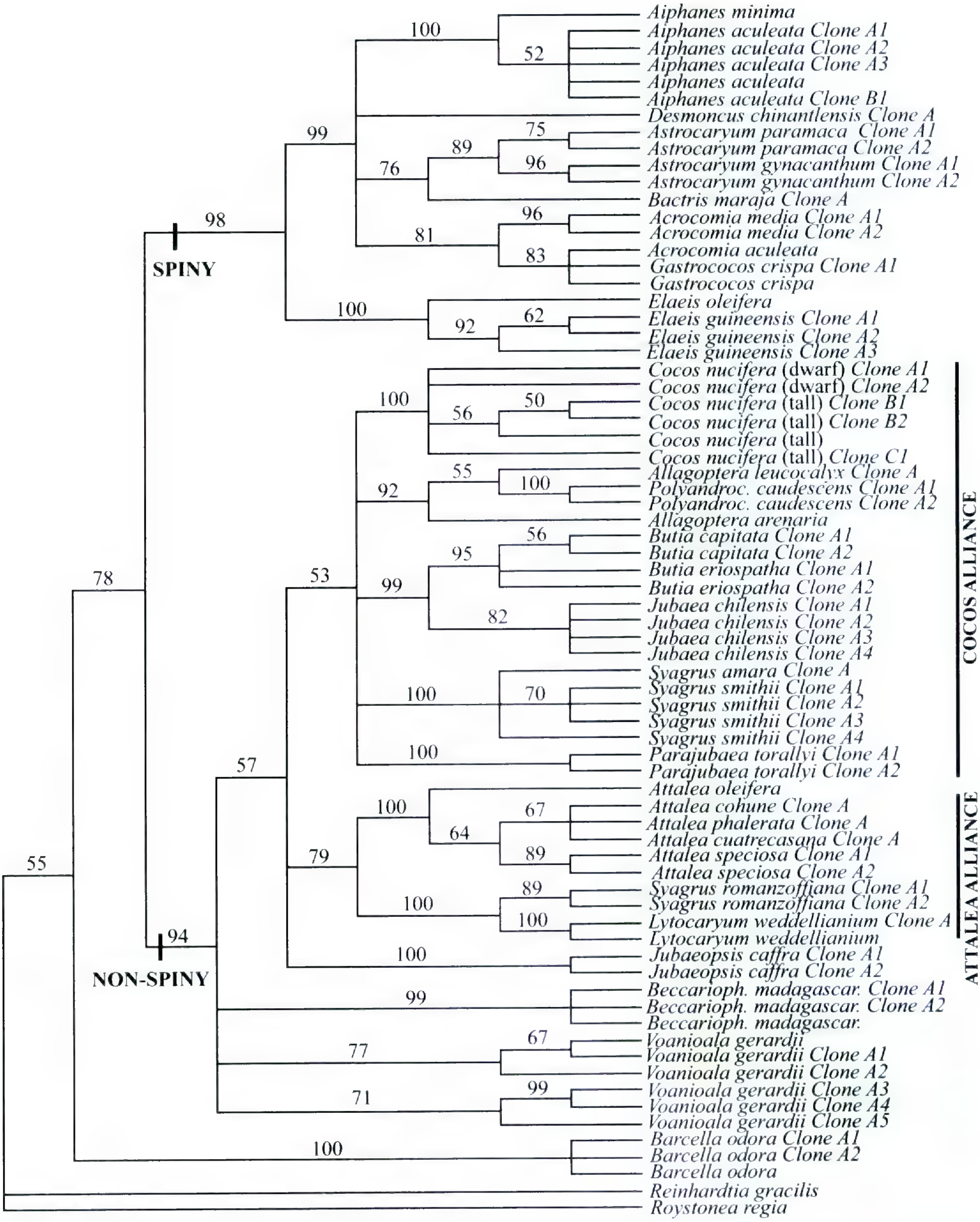

Figure 1. Maximum parsimony tree including clones. Strict consensus of 14,071 trees; tree length = 524; CI = 0.733; RC = 0.668; RI = 0.911. Percentages above branches show bootstrap values. The abbreviation *Beccarioph. madagascr.* = *Beccariophoenix madagascariensis*.

capitata is closely related to *B. eriospatha* (95% bs), both forming a well-supported sister group to *Jubaea chilensis* (99% bs). *Polyandrococos caudescens* is nested within the clade composed of *Allagoptera leucocalyx* and *A. arenaria* (92% bs). The Attalea alliance (79% bs) comprises the Attalea clade (100% bs) and its sister group, (*Syagrus romanzoffinana* + *Lytocaryum weddellianum*, 100% bs).

The spiny palms include *Elaeis* (2 species), *Ac-*

Table 2. Estimated divergence times of clades. N = node; F1 = Boulder Hill, New Zealand (42 mya), F2 = *Cocos intertrappeansis*, India (50 mya), Cocoeae fossils for setting minimum age constraints. Columns 1, 2, 3, and 4 represent the estimated times of divergence of the clades. *Cocos* alliance = (*Cocos nuccifera* + (*Allagoptera* + *Polyandrococos*) + (*Butia* + *Jubaea*) + (*Syagrus amara* + *S. smithii*) + *Parajubaea*). *Attalea* alliance = (*Attalea* + (*Syagrus romanzoffiana* + *Lytocaryum weddellianum*)). Outgroups: *Reinhardtia gracilis* and *Roystonea regia*.

Chronograms/mya	1	2	3	4
Outgroups: *Reinhardtia* and *Roystonea*	—	56.12(N1)	96.61(N1)	75.31(N1)
Cocoeae:	—	53.26(N2)	61.09(N2)	60.71(N2)
Spiny/non-spiny divergence	60.45(N1)	50(F2)	50(F2)	50(F2)
Non-spiny clade	51.02(N25)	43.07(N4)	42.88(N5)	42.93(N6)
Spiny clade	42(F1)	46.29(N43)	46.28(N44)	46.28(N45)
Malagasy clade	42.06(N26)	39.64(N5)	39.42(N6)	39.48(N7)
Jubaeopsis caffra	35.72(N50)	37.84(N6)	37.62(N7)	37.68(N8)
Cocos alliance	37.64(N27)	34.16(N19)	33.96(N20)	34.01(N21)
Attalea alliance	34.87(N51)	37.84(N6)	37.62(N7)	37.68(N8)
Parajubaea torallyi	29.87(N33)	29.62(N21)	29.44(N22)	29.48(N23)
Cocos nucifera	22.20(N35)	26.84(N22)	26.67(N23)	26.71(N24)
Elaeis guineensis + *E. oleifera*	—	42(F1)	42(F1)	42(F1)

Comparisons of estimated times of divergences of clades from chronograms (not shown) 1 and 2, 3, and 4 using different fossil calibration points.

rocomia (2) plus *Gastrococos*, *Bactris* plus *Astrocaryum* (2), *Desmoncus*, and *Aiphanes*. *Elaeis* is monophyletic (100% bs; *E. guineensis* +*E. oleifera*) and is sister to the rest of the spiny group (100%). *Acrocomia* (81% bs) is paraphyletic, with *Gastrococos crispa* forming a clade with *Acrocomia aculeata* (83% bs). Species of *Astrocaryum* and *Bactris* form a clade (76% bs). The three species of *Aiphanes* form a monophyletic group (100% bs). The position of *Desmoncus chinantlensis* is unresolved.

The ML tree (Fig. 2) had a -ln = 3824.8914. From the MODELTEST 3.06, HKY + G model was selected as the best model of substitution. Base frequencies used were: freq. A = 0.2948, freq. C = 0.1990, freq. G = 0.2256, and freq. T = 0.2806. The Ti/tv ratio was 1.8755 and the gamma distribution shape was 1.0177. MODELTEST also calculates the Aikaike Information Criterion (AIC), which compares unnested models of evolution. The model selected was TVM+G and the AIC was 7670.2085.

The ML (Fig. 2) and Bayesian (Fig. 3) analyses recovered trees that were consistent with the MP topology. They also show Cocoeae separated into non-spiny and spiny clades (100% prior probability), and the taxa have the same relative positions as in the MP tree.

Barcella is basal in Cocoeae, but is on a very long branch (0.117 substitution/site); its basal position is well supported in the Bayesian topology (94% posterior probability). The two Malagasy Cocoeae, *Beccariophoenix* and *Voanioala*, are basal and sister to the non-spiny group (99% posterior probabilty (pp)) in both topologies MP and Bayesian. *Jubaeopsis* appears to be sister to the Attalea alliance clade in the ML topology with no significant support, but is only weakly supported in the Bayesian analysis. *Attalea* is monophyletic (100% pp) and is sister to *Syagrus romanzoffiana* plus *Lytocaryum weddellianum* (100% pp), as also in the ML tree. The branches separating most taxa within the Cocos alliance are short, and this lack of resolution is also reflected in the Bayesian analysis. The basal branch (0.003 substitution/site) within this clade is formed by (*Syagrus smithii* + *S. amara*). There is robust support for the sister relationship of this clade (100% pp). Relationships among the three taxa *Allagoptera arenaria*, *A. leucocalyx*, and *Polyandrococos caudescens* are fairly well supported (0.006 subs./site) as in the MP (92% bs) and Bayesian (100% pp) topologies. *Jubaea chilensis* was sister to *Butia eriospatha* and *B. capitata*, and this clade is also well supported in both the MP (99% bs) and Bayesian trees (100% pp). *Cocos* and *Parajubaea* are joined on a very short branch (0.001 subs./site). *Parajubaea* is on a branch with 0.023 subs./site and in a clade with *Cocos nucifera* (0.035 subs./site); in both MP and Bayesian analysis (100% bs, pp) the dwarf form is also basal.

The two *Elaeis* species form a monophyletic group (0.037 subs./site; 100% posterior probability) and are basal in this clade as also observed in the MP analysis. The monophyly of Bactridinae (*Acrocomia*, *Aiplanes*, *Astrocaryum*, *Bactris*, *Desmoncus*, *Gastrococos*, Table 1) is again indicated (0.016

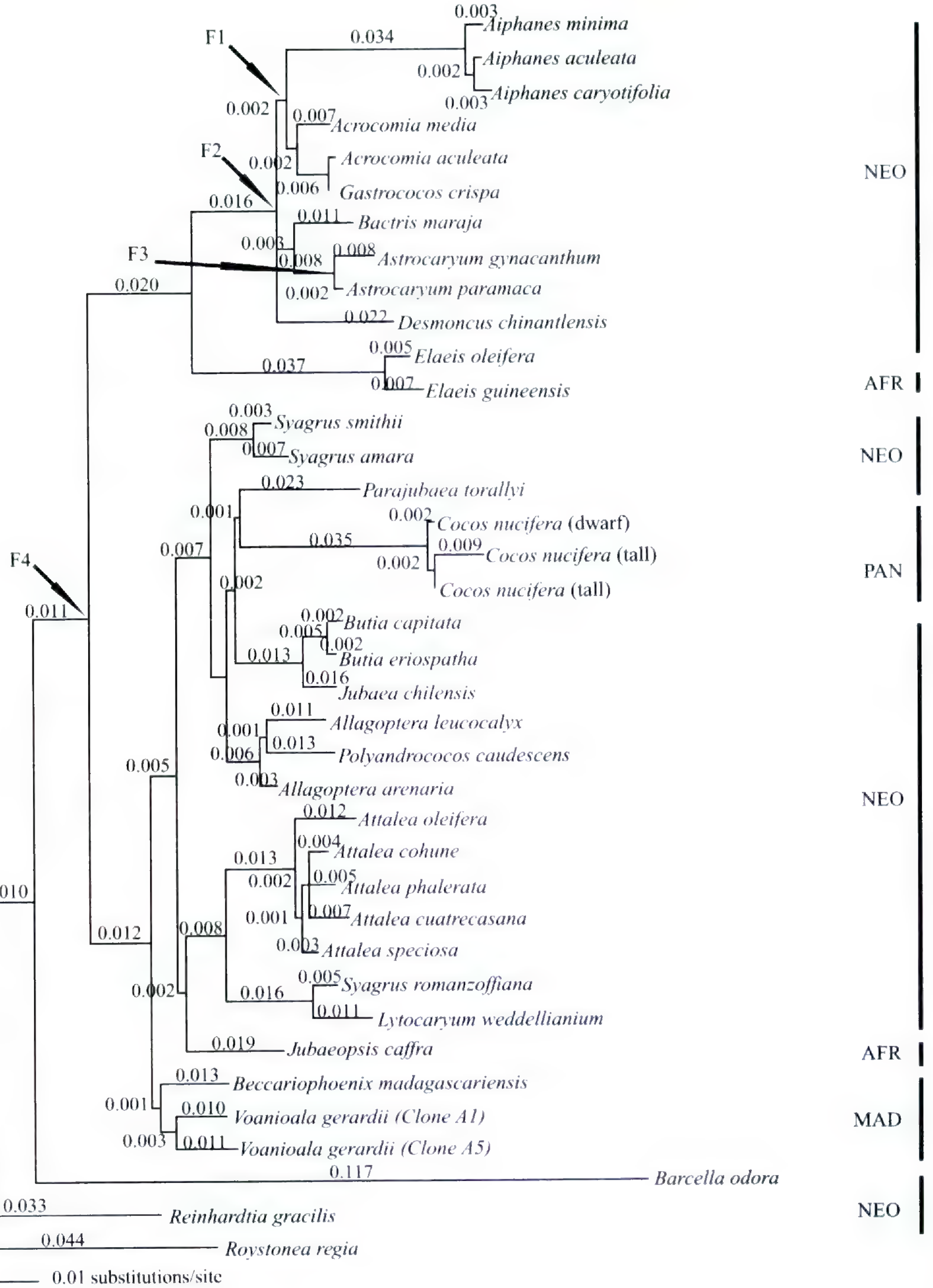

Figure 2. Maximum likelihood tree. Model used = HKY + G; base frequencies: A = 0.2948, C = 0.1990, G = 0.2256, T = 0.2806. Transition/transversion ratio = 1.8755; gamma distribution shape = 1.0177; Aikaike Information Criteria (AIC) = 7670.2085. Values above branches show number of nucleotide substitutions/site. F1, F2, and F3 = Cocoeae fossils. F1 = Wharekuri, New Zealand (32 mya). F2 = Boulder Hill, New Zealand (38–45 mya). F3 = Waihao beaked, New Zealand (27–31 mya). F4 = *Cocos intertrappeansis*, India (50 mya).

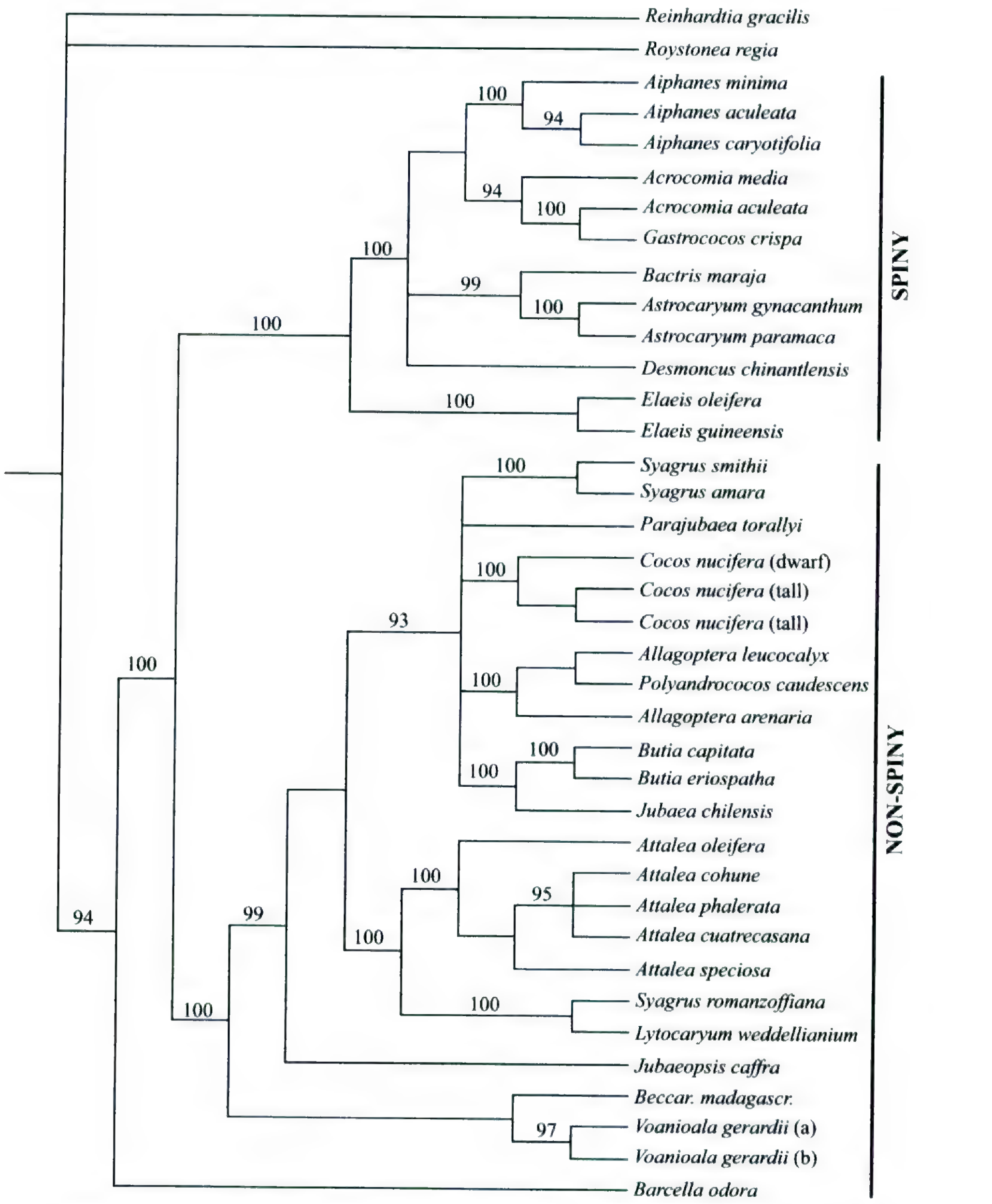

Figure 3. Bayesian Tree. Values above branches show percentages of prior probability. The abbreviation *Beccar. madagascr.* = *Beccariophoenix madagascariensis*.

subs./site; 100% pp). There is, however, not much further resolution within the Bactridinae. The branch leading to *Acrocomia media* and (*Acrocomia aculeata* + *Gastrococos*) is relatively short (0.002 subs./site; 94% posterior probability). There is reasonable support for an Acrocomia aculeata and Gastrococos crispa clade (100% pp, Fig. 3). *Bactris maraja* and *Astrocaryum* form a clade held by a short branch (0.003 subs./site), but that is well supported in the Bayesian tree (99% pp). *Aiphanes* forms a monophyletic group (100% pp, Fig. 3) with a branch length of 0.034 subs./site. In both the ML and Bayesian analyses, *Desmoncus chinantlensis* is unplaced within the Bactridinae.

The two outgroups *Reinhardtia* and *Roystonea* form the innermost node. The ML topology shows good support for nodes in the deeper parts of the tree, but weaker toward the terminals. In the Bayesian and ML analyses, there was better resolution within the Butiinae (sensu Uhl & Dransfield, 1987), showing a Cocos alliance (93% pp) and an Attalea alliance (100% pp).

Discussion

The MP, ML, and Bayesian topologies support division of Cocoeae into two major clades, generally corresponding to spiny and non-spiny taxa. Indeed, the presence of spines was used by Martius (1850: 277–304) for these groups to classify the Cocoinae into his "(i) *Genera aculeata*" [with spines] and "(ii) *Genera inermia*" [without spines]. The spines of *Bactris* and other members of the spiny clade are emergences from the epidermis of the whole palm. However, *Elaeis guineensis* and *E. oleifera*, basal in the spiny clade, have both fiber spines coming from the midribs of the lower pinnae of the leaf, and inflorescence spines, which are modified rachillae tips (Tomlinson, 1963). The non-spiny clade includes *Butia* and *Syagrus*, which may have petiolar spines, modified from leaf sheath fibers (Tomlinson, 1963). Spines appear to be homoplasious in Cocoeae.

Barcella odora appears to be basal in the Cocoeae and is sister to both the spiny and non-spiny cocosoid palms (Figs. 1, 3). *Barcella* is monotypic and is found only in the Amazon region in Brazil north of the Rio Negro growing on white-sand soils in Brazil. James Trail first described the palm in 1874 as *Elaeis* (subg. *Barcella* Trail), but it differs from *Elaeis* by its lack of petiole spines and its inflorescence borne on a long peduncle. The inflorescence is made up of either all staminate or both staminate and pistillate flowers, but an *Elaeis* inflorescence bears either staminate or entirely pistillate flowers. These differences led Drude to recognize *Barcella* as a distinct genus in the Palmae for *Flora Brasiliensis* (Henderson, 1986). However, like *Elaeis*, its flowers are large and are sunken in pits on the rachillae, whose tips may form sharp points. *Barcella* has been traditionally placed within subtribe Elaeidinae together with *Elaeis guineensis* and *E. oleifera* (Uhl & Dransfield, 1987). A Templeton (Wilcoxon signed-ranked) test showed that there was no significant difference between the two MP topologies when *Barcella* was constrained into a clade with *Elaeis* ($P > 0.05$, $n = 17$). This suggests that Elaeidinae may not be polyphyletic and that *Barcella* may be a member of the spiny clade, its rachillae tips being the modified "spines" that would then characterize this subtribe.

Chromosome studies of the spiny clade show that they have a haploid number of 15 (Read, 1966; Röser, 1999) except for *Elaeis*, which has $n = 16$. On the other hand, all members of the non-spiny clade have $n = 16$ except for *Beccariophoenix madagascariensis* ($n = 18$), perhaps *Jubaeopsis caffra* ($n = 80$–100) (Read, 1966), and *Voanioala gerardii* ($n = 298$) (Johnson et al., 1989), a probable autopolyploid. *Voanioala* is basal in the non-spiny Cocoeae, and its chromosome number is the highest recorded for monocotyledons. *Voanioala gerardii* is a large, slow-growing palm restricted to Madagascar, suggesting that it is an evolutionary relict which has undergone successive mitotic doublings or selfing of unreduced gametes to form a reproductively isolated high autopolyploid (Johnson et al., 1989). In the ML and Bayesian analyses for *V. gerardii*, two divergent sequences were isolated from the clones and in both topologies they show a sister relationship to one another with good support (97% pp, Fig. 3). In the MP topology they form a basal trichotomy in the non-spiny clade with *Beccariophoenix*.

Beccariophoenix madagascariensis plus *Voanioala gerardii* are basal in the non-spiny clade. Like *Voanioala*, *Beccariophoenix* is endemic to Madagascar growing in the white-sand and submontane rain forests. Formerly thought to be a member of the Areceae by Beccari and Pichi-Sermolli (1956) and Moore (1973a), it was placed in the Cocoeae by Uhl and Dransfield (1987), based on the synapomorphies of its woody and beaked peduncular bract and three endocarp pores. The inflorescences are massive and torpedo-like borne on a long peduncle. The fruit is single-seeded, purple-brown with a thin but woody endocarp. In its root anatomy, it has the same single-layered, unevenly thickened tanniniferous exodermis as in Cocoeae (Seubert, 1998a).

Jubaeopsis caffra has an unresolved position within the Cocos and Attalea alliances; however, it may be basal in the clades formed by these alliances (57% bs: see Figs. 1, 2). Its morphology closely resembles that of *Jubaea* and *Butia*, differing from *Jubaea* by its clustering habit, non-stalked staminate flowers, and separate sepals and from *Butia* in its many stamens (18) and lack of petiolar spines. The three are similar in having lateral pores on their endocarps, a rhizodermis with large unevenly thickened cells, and exodermis with tanniniferous, evenly thickened cells (Seubert, 1998a). *Jubaeopsis* is monotypic, endemic to East Pondoland, South Africa; it is also a polyploid ($2n = 160$–200: Read, 1966).

Lytocaryum weddellianum is closely related to *Syagrus romanzoffiana* (100% bs, 100% pp, Figs. 1, 3) and forms a clade in the Attalea alliance. *Lytocaryum* is restricted to southeastern Brazil and is similar to *Syagrus romanzoffiana* in having endocarps with three internal shiny vertical lines and basal pores, but differs in its thin endocarp. Although there is good molecular and morphological

evidence for the synonymy of *Lytocaryum* with *Syagrus* (Henderson et al., 1995; cf. Figs. 1–3 herein), the formal reduction of *Lytocaryum* is not proposed here. *Syagrus* is a large complex genus of 30 species and appears to be polyphyletic with *S. amara* + *S. smithii* forming a clade in the Cocos alliance and the type species, *Syagrus cocoides*, has not been sequenced.

The five species of *Attalea* studied form a monophyletic group. *Attalea* is a large Neotropical genus of 29 species that possess distinctive inflorescence types, with individuals bearing either staminate or androgynous flowers (Glassman, 1999). Previously six genera, *Attalea*, *Markleya*, *Maximiliana*, *Orbignya*, *Parascheelea*, and *Scheelea*, were recognized (Glassman, 1999; Henderson & Balick, 1991) based on characters of the stamens and petals of the male flowers. Molecular evidence here shows that these genera differ from each other by only one or two bp positions. *Attalea* (s.l.) has a fairly homogeneous root anatomy (Seubert, 1998b) and pollen morphology (Thanikaimoni, 1971); this, together with the lack of other distinguishing morphological (Tomlinson, 1961) and now molecular characters, suggests that this group should be united into one genus, *Attalea*.

The closest relative to *Cocos nucifera* is still unresolved, but this species probably belongs to the clade referred to here as the Cocos alliance, comprising *Allagoptera* plus *Polyandrococos*, *Butia* plus *Jubaea*, *Syagrus smithii* plus *S. amara*, and *Parajubaea*. All these palms occupy habitats with low rainfall and sandy soils. *Allagoptera arenaria* grows in the restinga, and *Polyandrococos caudescens* is found in open lowland areas within the Brazilian Atlantic coastal forest (Lorenzi et al., 1996; Henderson et al., 1995). *Butia* is found in southern subtropical South America and *Jubaea* is endemic to Chile. *Parajubaea* is found in Bolivia, Ecuador, and southern Colombia. *Syagrus amara* is native to the Lesser Antilles and found in coastal ravines, while *Syagrus smithii* is found on lowland forest on non-inundated soils in northwestern South America. *Cocos nucifera* is a strand plant with wide distribution throughout the tropics.

The three sequences for *Cocos nucifera* were taken from one dwarf and two tall forms of the coconut (sensu Narayana & John, 1949). They were cultivated from the Pacific and Melanesia (region occupied by Melanesian people). They form a monophyletic group (100% bs), but subtended by a moderately long branch (0.035 subs./site). *Cocos nucifera* may perhaps be more closely related to *Parajubaea* than to other members of the Cocos alliance. In the ML analysis, *Parajubaea torallyi* resolved as sister to *Cocos nucifera*, but on a very short branch; two nucleotide bases are in common between the two supporting this branch. *Parajubaea torallyi* grows naturally in the humid valleys of sandstone mountains of the central and southern Bolivian Andes at approximately 2000 m altitude (Uhl & Dransfield, 1987; Moraes, 1996). This Bolivian palm has been relatively unknown since its original description by Martius (1847a, as *Diplothemium*). Since then it has been shifted to *Jubaea* (Wendland, 1878), *Allagoptera* (Kuntze, 1891), and *Polyandrococos* (Barbosa Rodrigues, 1901). Max Burret (1930) proposed the name *Parajubaea* for this genus with *P. cocoides*, a cultivar found in Ecuador (see Moraes & Henderson, 1990), as the type. *Parajubaea* was placed in the Butiinae by Uhl and Dransfield (1987) based on its similarity to *Jubaea* and *Syagrus*, and indeed, morphological differences between them are very slight. *Parajubaea* has 13 to 18 stamens, whereas *Jubaea* has 18 and *Syagrus* has 6. The endocarp of *Parajubaea* bears ridges, while it is crested in *Jubaea*. Moraes and Henderson (1990) also noted that the rachillae of *Parajubaea cocoides* have small side branches, not seen in the rest of the Butiinae (sensu Uhl & Dransfield, 1987). The mesocarp is fleshy and fibrous, and the fruits of *Parajubaea* are dispersed by riverine and animal means (Vargas, 1994).

Allagoptera is closely related to *Polyandrococos* (92% bs, 100% pp, Figs. 1, 3), and both share the synapomorphy of spicate inflorescences. *Allagoptera* includes four species, all acaulescent and with dichotomous branching subterranean stems (Tomlinson, 1967). The distinctive irregularly grouped pinnae inserted at various angles characterize three of the four species as well as *Polyandrococos caudescens* (Mart.) Barb. Rodr. The cuticle has a waxy layer, and there is also a woolly tomentum. Waxy cuticles are also found in *Syagrus amara* (Jacq.) Mart. and *Polyandrococos caudescens*. The strong molecular as well as morphological evidence suggests that monotypic *Polyandrococos caudescens* belongs in *Allagoptera*.

Both morphological and molecular evidence suggests the sister relationship of *Butia* and *Jubaea chilensis* (see also Glassman, 1987; Uhl & Dransfield, 1987; Henderson et al., 1995). *Butia* differs from *Jubaea chilensis* in having 6 instead of 18 stamens, unclustered pinnae, with usually oblique split tips of the pinnae versus acuminate symmetrical tips, and in petiolar spines present versus none. The fruits of *Butia* may be one- to three-chambered, as in *Butia capitata*, but are usually one-chambered in *Jubaea*. The Chilean wine palm, *Jubaea chilensis*, is monotypic and endemic to

Chile. The close relationship between *Butia* and *Jubaea* is further corroborated by similarities in leaf (Glassman, 1987) and root anatomy (Seubert, 1998), possession of smooth or striate spathes, and the embryo pores in the equatorial position on the endocarp.

Syagrus (30 spp. sensu Henderson et al., 1995) is predominantly a South American genus, with one species (*S. amara*) found in the Lesser Antilles. It is most speciose in Brazil (22 spp.), where it is one of the main plants of the cerrado and campo rupestre. Its taxonomic history has been closely linked with *Cocos*, and taxa have been transferred from *Syagrus* to *Cocos*. For example, *Syagrus sancona* H. Karsten (1856) was shifted to *Cocos sancona* (H. Karsten) Hook. f. (1882) and back again to *Syagrus sancona* (H. Karsten) Hook. f. (Glassman, 1979). Similarly, *Cocos amara* Jacq. (1763) was transferred to *Syagrus amara* (Jacq.) Mart. (1847b), to *Rhyticocos* (Jacq.) Becc. (1886), and to *Syagrus amara* by Glassman (1970). Molecular evidence (herein) suggests that *Syagrus* may be polyphyletic. However, *Syagrus amara* and *S. smithii* form a clade with strong support (100% bs and pp). The fruits of these two *Syagrus* are elliptical with prominently ridged endocarps with basal pores and ruminate endosperm.

In the spiny group, subtribe Bactridinae is monophyletic herein in all three topologies and includes *Aiphanes*, *Acrocomia*, *Gastrococos*, *Bactris*, *Astrocaryum*, and *Desmoncus*. These Neotropical palms are characterized by their emergent spines and fruits with hardened endocarps.

Species of *Aiphanes* (22) are very spiny understory palms found predominantly in the Antilles and western South America (Borchsenius & Bernal, 1996). The genus is monophyletic herein (100% bs, Fig. 1), with several distinctive morphological characters within Cocoeae: praemorse pinnae, staminate and pistillate flowers with free sepals, and protandrous inflorescences.

Both species of *Acrocomia* and *Gastrococos crispa* form a well-supported clade in the MP and Bayesian trees (81% bs, 94% pp, Figs. 1, 2). There is good indication that *Acrocomia aculeata* and *Gastrococos crispa* are closely related (83% bs, 100% pp, Figs. 1, 3) differing by only two bp positions. The genus *Acrocomia* is native from the West Indies to southern Brazil, and was erected by Martius in 1824 for a single species (*A. aculeata*). Since then 25 species have been added, with Beccari (1912) recognizing 15 species, but there has been no subsequent systematic revision of this genus since Bailey (1941). Species of *Acrocomia* are heavily armed, tall palms with a crown of plumose-like pinnate leaves. They inhabit dry, non-inundated regions with impoverished soils, and their fruits are commonly dispersed by cattle. *Gastrococos crispa* is monotypic and endemic to Cuba and is vegetatively similar to *Acrocomia*, the two differing mainly in floral arrangement and morphology. The pollen of the two genera are very similar, differing only in size (Thanikaimoni, 1971).

Bactris currently contains some 73 species growing mostly in Central and South America (Henderson, 2000). In my analyis, it is sister to the Astrocaryum clade (*Astrocaryum paramaca* + *A. gynacanthum*), with which it shares several characteristics (76% bs, 99% pp, Figs. 1, 3). It may be distinguished by the lower surface of the pinna being pale gray-green not white tomentose as in *Astrocaryum*, with the exception of *Bactris bidentula* and *B. glaucescens* (Henderson, 2000).

All but one species of *Desmoncus* are armed with climbing hooks and represent the New World ecological equivalent of the rattans (Calamoideae, Arecaceae), although there is no close phylogenetic relationship between the two.

Elaeis has two closely related species (100% bs and pp, Figs. 1, 3), forming the basal clade in the spiny cocosoid palms. *Elaeis* may be distinguished by its unisexual inflorescences with flowers borne in shallow pits on the spiny rachillae. *Elaeis guineensis*, the economically important oil palm, and *Elaeis oleifera* are interesting because they are the only Cocoeae that are distributed both in Africa and South America, respectively. These two taxa may represent the Gondwanan relationships of the Cocoeae (see Thanikaimoni, 1971).

Times of Divergence

The divergence times among the spiny cocosoid palms were not easily discernible due to the polytomy at the node subtending the Bactridinae. The divergence time for the split of the spiny and the non-spiny Cocoeae lineages was estimated to be around 50–60 mya. The two Madagascan monotypic endemics, *Beccariophoenix* and *Voanioala*, seemed to have diverged from the rest of the non-spiny lineages about 40–51 mya. The Cocos alliance group diversified from the Attalea alliance group apparently about 40 mya. *Cocos nucifera* seems to have diverged from its sister lineage *Parajubaea* about 22–27 mya. *Jubaeopsis caffra*, endemic to Pondoland, southeast Africa, diverged from its sister lineage around 36–38 mya.

Cocoeae Fossils

The earliest unequivocal palm fossil record is from the Upper Cretaceous Magothy Formation of

Santonian (84 mya) (Daghlian, 1981). According to Moore (1973b) and Raven and Axelrod (1974), palms may have originated in West Gondwana—Africa, South America, and part of Antarctica. *Palmoxylon patagonicum* was found in Chubut Province, Argentina (Romero, 1968). Cocoeae trichotomosulcate pollen is observed frequently only in *Acrocomia*, *Gastrococos*, and *Elaeis* (Thanikomoni, 1971; M. Harley, pers. comm.). Pollen characteristic of *Acrocomia* type 3 and known as *Trichotomosulcites antiquus* was reported from the Maastrichtian (65 mya) of Germany by Krutzsch and Lenk (1969). They described it as having a reticulate exine and a clearly differentiated simple tectate margin next to the aperture. Although *Acrocomia* has trichomosulcate pollen, it has coarsely perforated exine; on the other hand, *Gastrococos* has exclusively trichomosulcate pollen with reticulate exine, but the aperture margin is not well differentiated (M. Harley, pers. comm.). *Elaeis* pollen is known from the Miocene (11–22.5 mya) from West Africa (Muller, 1981).

A fossil of middle Eocene age, *Astrocaryum olssoni*, was discovered by A. Olsson in Negritos in northwestern Peru. These calcified asymmetrical nuts range from 3.75 to 5.25 cm in length and 2.5 to 3.75 cm in diameter and have a fibrous outer layer, an inner layer 2–3 mm thick, and an interior filled with structureless calcified material (Berry, 1926a). Other fossil endocarps aged between 12 and 45 Ma have been found in Boulder Hill, Otago, and Wharekuri, Canterbury, New Zealand; they are 3.5–12 cm long and have distinctive Cocoeae pores (Campbell et al., 2000). Berry (1926b) and Couper (1952) reported *Cocos*-like fossils from Cooper's Beach, Mangonui, Auckland, New Zealand, that are from the Miocene period. The endocarps of the fossil *Cocos zeylandica* (15–12 mya) resemble closely those of the extant *Parajubaea torallyi* (Campbell et al., 2000). Fliché (1896) described a fossil fruit named *Cocopsis* from the Argonne of France of Miocene age.

Fossil *Cocos* fruit from Chinchilla Sand, Queensland (Australia), of the latest Pliocene (2 mya), most resembles the extant *Cocos nucifera* (Rigby, 1995). The silicified fruit (10 cm long × 9.5 cm max. diam.) with three pores was also associated with other silicified palmwood and megafauna bones. Kaul (1951) recorded *Cocos sahni* embedded in diatomous deposits from the early Tertiary (Eocene) in the mines at Kapurdi, Western Rajasthan, India. Patil and Upadhye (1984) described a petrified fruit of *Cocos intertrappeansis* from the Tertiary of Mohgaonkalan, Madhya Pradesh. Tripathi et al. (1999) illustrated a fossil fruit very similar to *Cocos nucifera* from the Tertiary of Amarkantak, Madhya Pradesh. It is much larger than the others from India, measuring 13 × 10 × 6 cm with a thin epicarp, wide and fibrous mesocarp, and well-developed hardened endocarp.

The now extinct *Paschalococos disperta* from Easter Island was described by Dransfield et al. (1984). Its fruits are very similar to those of the extant *Jubaea chilensis* from Chile. About 30 partially gnawed endocarps were discovered in the cave floor near Ana Okeke, Easter Island. Four of the best preserved fruits are about 2.5 × 3 cm, with smooth endocarps and three equatorially placed pores. Radiocarbon dating aged them at about 820 ± 40 years B.P.

Biogeography

This well-documented Cocoeae fossil assemblage suggests that *Cocos nucifera* is part of a lineage of palms with former worldwide distribution. At present most Cocoeae (201 species) are centered in the Neotropics, with four species in the Old World (Africa and Madagascar), while *Cocos nucifera* is pantropical. The origin of the coconut has been a controversial issue for more than a century because of this biogeographical distribution. Alphonse de Candolle (1886) and Cook (1910) proposed a New World origin, Beccari (1963) claimed an Asiatic or Polynesian origin, Moore (1973b) presented evidence for a Melanesian origin, Harries (1978) postulated that the coconut originated in the Western Pacific. The question of dispersal by water and humans further complicates matters. Here, I attempt to reconstruct the evolutionary history of Cocoeae and in particular of the coconut. Estimated times of divergence of the Cocoeae clades in the ML tree using the Non Parametric Rate Smoothing (NPRS) analysis (Sanderson, 2002) are calibrated with fossil fruits, and the geographical distribution of Cocoeae is mapped on the maximum likelihood tree to suggest a possible model for the origin of *Cocos nucifera*.

The Malagasy clade (*Beccariophoenix* and *Voanioala*) and the African *Elaeis guineensis* are both basal in all analyses herein (Figs. 1–3) in the non-spiny and spiny clades, respectively. Beyond this clade, the majority of the non-spiny and spiny clades are Neotropical. Basal to these two groups is *Barcella*, a South American endemic Cocoeae. Both outgroups, *Reinhardtia* (subtribe: Malortieinae) and *Roystonea* (subtribe: Roystoneinae), are Neotropical and belong to the palm tribe Areceae. The topology therefore suggests a Neotropical origin for the Cocoeae and for the wild progenitors of *Co-*

cos nucifera. This hypothesis may be tested with the times of divergence of the clades and tectonic events.

At circa Eocene (55–37 mya) fossil Cocoeae fruits were present in South America, New Zealand, and India; Miocene (22–5 mya) endocarps have been found in New Zealand and Africa, Pliocene (5–2 mya) fruits in Australia and India, and recent partial endocarps (800 years old) on Easter Island. By the Eocene Cococeae were already in existence, and therefore probably arose as a lineage sometime earlier, quite possibily the late Paleogene (65–60 mya) since palms were already well diversified as evidenced by the fossil records (Raven & Axelrod, 1974; Muller, 1979; McLoughlin, 2001).

The chronogram (not shown) from the NPRS analysis suggests that the spiny and non-spiny cocosoids diverged between 50 and 60 mya. Independent estimates herein of the ages of these sister clades are approximately the same, that of the former ranging from 42 to 46 mya and of the latter, 42 to 43 mya. The two Malagasy genera *Beccariophoenix* and *Voanioala* diverged from the rest of the non-spiny group ca. 40–51 mya (see herein, Table 2). The Madagascar block began separating from Africa at about 90 mya, but there was possibly a connection between Madagascar and Africa until the middle Oligocene (McLoughlin, 2001). The next cladogenesis was approximately 42 mya (see herein, Table 2), when the Cocos alliance became differentiated from the Attalea alliance clade. *Jubaeopsis caffra*, the South African endemic, is within this large non-spiny clade and estimated to have diverged from the rest of the group about 36–38 mya. As South America and Africa had been separated by then, ca. 95–100 mya (Goldblatt, 1993: 23), it is quite possible that *Jubaeopsis* arrived in Africa by long-distance dispersal. The fruit (2–4 cm long) looks like a miniature coconut and possesses a thin fibrous mesocarp covering a hard inner endocarp. It is restricted near the estuarine banks of the Metentu, Msikaba, and Mzinlaua Rivers of the eastern coast of South Africa (Tuley, 1995). The distance between the southern tip of South America and that of South Africa was not great during the Eocene (Goldblatt, 1993), and the ocean currents were moving westward (Axelrod & Raven, 1978).

Within the Cocos alliance, the age of the node (chronogram, not shown) subtending *Parajubaea* is at least 29.87–29.44 million years, and the node closest to it subtending the crown group of *Cocos nucifera* is aged at 22.20–26.84 million years (see Table 2). Thus the minimum age of divergence of *Parajubaea* and *Cocos nucifera* is approximately 23 million years. This finding suggests that the coconut belongs to an ancient lineage with its wild progenitors occurring in the Neotropics, and it may be possible that *Cocos nucifera* is the only extant species of this lineage. Rigby (1995) reported a *Cocos nucifera* fossil in Chincilla Sand, Queensland (Australia), of Pliocene age (2 mya). This large fossil *Cocos* has the three pores at one end distinctive of the cocosoid palms. This also eliminates any action of humans in the original distribution of *Cocos nucifera*, although the dispersal of it in the Pacific in recent times was partly the responsibility of humans. At the time of divergence of the putative progenitors of the *Cocos nucifera*, separation of South America from West Antarctica had already taken place (30 mya) as the Powell Basin opened up the Scotia Sea to create the Drake Passage (Hallam, 1981). The geological ages of the Cocoeae endocarp fossils found in New Zealand fall into two groups—Eocene and Miocene. The Eocene group found on the eastern side of the South Island is postulated here to have arrived from South America via the Antarctic land bridge, but the Miocene group found on the northern shores of the North Island persisted till much later when New Zealand moved northward resulting in subtropical climes in the North Island during the Miocene. The emergence of volcanic archipelagoes to the north enabled the exchange of subtropical taxa to and from New Zealand (Raven & Axelrod, 1972).

The early lineage of *Cocos nucifera* most likely possessed some means of water dispersal. The fruit of *Cocos nucifera* differs most prominently from those of other Cocoeae in its large size, thick layer of fibrous mesocarp, and its large endocarp with a huge cavity lined with a layer of hard endosperm and filled with liquid endosperm. This adaptation for floating and the enclosed vessel protecting the developing embryo would probably enable it to cross ocean barriers and establish successfully. Edmonson (1941) suggested that the coconut can float in the ocean for up to three months and still be viable.

It may be hypothesized that Cocoeae may have originated in South America during the Paleogene, diversified and spread eastward to Africa, Madagascar, and India and southward to Australasia and New Zealand through the western Antarctic corridor (till the Oligocene). The putative progenitors of the coconut were from South America and became widely distributed in the Old World by long-distance water dispersal. The Deccan Traps of India have a well-studied paleobotanical flora (Prakash, 1958) and show affinities to those of the Gondwanan continents. It is postulated that Cocoeae migrated to India from Madagascar after the diver-

gence of the basal clade via long-distance dispersal as the fossil endocarps found in India were of lower Eocene age, when India had already separated from Madagascar. These fossils were described as having fibrous mesocarps (see Patil & Upadhye, 1984, and Tripathi et al., 1999).

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Appendix 1. Species sequenced and collection data. Sampling method: Every extant known palm genus (20) in the Cocoeae was sampled. In several genera two or more taxa were listed. One dwarf and two tall forms of *Cocos nucifera* were sequenced.

Taxon	Herbarium voucher	GenBank access. no. *prk*
Extant:		
Acrocomia aculeata (Jacq.) Lodd.	Brazil, *Henderson AH 3057* (NY)	AY601224
Acrocomia media O. F. Cook	Puerto Rico, *Gunn 2* (MO)	AY601222 (Clone A1) AY601223 (Clone A2)
Aiphanes aculeata Willd.	Brazil, *Henderson AH 3072* (NY)	AY601210 AY601211 (Clone B)
Aiphanes caryotifolia (Kunth) H. Wendl. syn. *Aiphanes aculeata*	Brazil, *Gunn 90* (MO)	AY601207 (Clone A1) AY601208 (Clone A2) AY601209 (Clone A3)
Aiphanes minima (Gaertn.) Burret	Cuba, *Gunn 95* (MO)	AY601206 (Clone A1)
Allagoptera arenaria (Gomes) Kuntze	(Lewis & Doyle, 2002)	AF453331
Allagoptera leucocalyx (Mart.) Kuntze	Brazil, *Gunn 93* (MO)	AY601242 (Clone A1)
Astrocaryum gynacanthum Mart.	French Guiana, *Torke 239* (MO)	AY601227 (Clone A1) AY601228 (Clone A2)
Astrocaryum paramaca Mart.	French Guiana, *Torke 238* (MO)	AY601213 (Clone A1) AY601229 (Clone A2)
Attalea cohune Mart.	Belize, *Gunn 89* (MO)	AY601239 (Clone A)
Attalea cuatrecasana (Dugand) Henderson, Galeano & Bernal	Colombia, *Henderson AH 3069* (NY)	AY601241 (Clone A)
Attalea oleifera Barb. Rodr.	Brazil, *Noblick 5133* (MBC)	AY601238
Attalea speciosa Spreng.	Brazil, *Henderson AH 3067* (NY)	AY601245 (Clone A1) AY601246 (Clone A2)
Attalea phalerata Spreng.	Brazil, *Noblick 5018* (MBC)	AY601240 (Clone A)
Bactris maraja Mart.	Colombia, *Bernal, Galeano, Sanders 1096* (FTG)	AY601214 (Clone A)
Barcella odora (Trail) Drude	Brazil, *Kahn 3608* (CEN)	AY601215 (Clone A1) AY601216 (Clone A2) AY601217
Beccariophoenix madagascariensis Jum. & H. Perrier	Madagascar, *Noblick 5065* (MBC)	AY601236 (Clone A1) AY601237 (Clone A2)
Butia capitata (Mart.) Becc.	Brazil, *Henderson AH 3064* (NY)	AY601251 (Clone A1 AY601252 (Clone A2)
Butia eriospatha (mart.) Becc.	Brazil, *Gunn 87* (MO)	AY601253 (Clone A1) AY601254 (Clone A2)
Cocos nucifera L. (dwarf)	Cult. (tropical Melanesia), *Gunn 85* (MO)	AY601230 (Clone A1) AY601231 (Clone A2)
Cocos nucifera L. (tall)	Cult. (Pacific), *Gunn 86* (MO)	AY601232 (Clone B1) AY601233 (Clone B2)
Cocos nucifera L. (tall)	Pacific, *Henderson AH 3063* (NY)	AY601234 (Clone C) AY601235
Desmoncus chinantlensis Liebm. ex Mart.	Guatemala, *Hubbuch & Aronson 120* (FTG)	AY601212 (Clone A)
Elaeis guineensis Jacq.	Cult. (MBC), *Gunn 88* (MO)	AY601219 (Clone A1) AY601220 (Clone A2) AY601221 (Clone A3)
Elaeis oleifera (Kunth) Cortés	South America, *Gunn 94* (MO)	AY601218
Gastrococus crispa (Kunth) H. E. Moore	Cuba, *Zona 614* (FTG)	AY601225 (Clone A) AY601226
Jubaea chilensis (Molina) Baillon	Chile, *Henderson 3073* (NY)	AY601255 (Clone A1) AY601256 (Clone A2) AY601257 (Clone A3) AY601258 (Clone A4)
Jubaeopsis caffra Beccari	South Africa, *Brand 452* (NY)	AY601272 (Clone A) AY601273

Appendix 1. Continued.

Taxon	Herbarium voucher	GenBank access. no. *prk*
Lytocaryum weddellianum (H. Wendl.) Tol.	Brazil, *Henderson AH 3059* (NY)	AY601249 (Clone A) AY601250
Parajubaea torallyi (Mart.) Burret	Bolivia, *Vargas 3183* (NY)	AY601264 (Clone A1) AY601265 (Clone A2)
Polyandrococcos caudescens (Mart.) Barb. Rodr.	Brazil, *Noblick 5003* (MBC)	AY601243 (Clone A1) AY601244 (Clone A2)
Syagrus amara (Jacq.) Mart.	Dominica, *Noblick 4809* (MBC)	AY601259 (Clone A)
Syagrus romanzoffiana (Cham.) Glassman	Brazil, *Henderson AH 4210* (NY)	AY601247 (Clone A1) AY601248 (Clone A2)
Syagrus smithii H. E. Moore	Peru, *Noblick 96260* (MBC)	AY601260 (Clone A1) AY601261 (Clone A2) AY601262 (Clone A3) AY601263 (Clone A4)
Voanioala gerardii J. Dransf.	Madagascar, *Dransfield J. D. 6389* (K)	AY601266 AY601267 (Clone A1) AY601268 (Clone A2) AY601269 (Clone A3) AY601270 (Clone A4) AY601271 (Clone A5)
Outgroups:		
Reinhardtia gracilis	(Lewis & Doyle, 2002)	AF453372
Roystonea regia	(Lewis & Doyle, 2002)	AF453375
Fossil Fruits:		
F1 Wharekuri	New Zealand, *Fordyce OU 30758* (Otago Univ., Dunedin)	
F2 Boulder Hill	New Zealand, *Millan, Stillwell & Linquist OU 31113* (Otago Univ., Dunedin)	
F3 Waihao husk	New Zealand, *Gebneff, OU 39784* (Otago Univ., Dunedin)	
F4 *Cocos intertrappeansis*	India, *Patil* MOH/EVU/16 (Inst. Sci., Nagpur)	

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CONTENTS

Pollination Ecology of *Gaura* and *Calylophus* (Onagraceae, Tribe Onagreae) in Western Texas, U.S.A. ——— *Richard R. Clinebell II, Angela Crowe, David P. Gregory & Peter C. Hoch* 369

A Systematic Overview of Frankeniaceae and Tamaricaceae from Nuclear rDNA and Plastid Sequence Data ——— *John F. Gaskin, Farrokh Ghahremani-nejad, Dao-yuan Zhang & Jason P. Londo* 401

Revision of the Madagascan Endemic *Stapelianthus* (Apocynaceae) Based on Molecular and Morphological Characters ——— *P. V. Bruyns & C. Klak* 410

Phylogeny and Evolution of *Symbolanthus* and *Wurdackanthus* (Gentianaceae–Helieae) in the Guayana Highlands and Andes, Based on Ribosomal 5S-NTS sequences ——— *Katherine R. Gould & Lena Struwe* 438

VIII International Aroid Conference, Missouri Botanical Garden, St. Louis, 9–11 August 1999 Introduction ——— *Thomas B. Croat* 447

Synopsis of the Genus *Spathiphyllum* (Araceae) in Colombia ——— *Felipe Cardona* 448

Araceae from Central Brazil: Comments on Their Diversity and Biogeography ——— *Eduardo G. Gonçalves* 457

Progress in Ornamental Aroid Breeding Research ——— *R. J. Henny, D. J. Norman & J. Chen* 464

A Preliminary Survey of Petiolar Collenchyma in the Araceae ——— *Eduardo G. Gonçalves, Élder A. S. Paiva & Marcus A. Nadruz Coelho* 473

Vegetative Anatomical Data and Its Relationship to a Revised Classification of the Genera of Araceae ——— *Richard C. Keating* 485

Systematic Occurrence of Raphide Crystals in Araceae ——— *Richard C. Keating* 495

The Phylogeny of the Cocoeae (Arecaceae) with Emphasis on *Cocos nucifera* ——— *Bee F. Gunn* 505

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AFRICA'S HOTSPOTS OF BIODIVERSITY REDEFINED[1]

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ABSTRACT

A key problem for conservation is the coincidence of regions of high biodiversity with regions of high human impact. Twenty-five of the most threatened centers of plant diversity were identified by Myers et al., and these "hotspots" play a crucial role in international conservation strategies. The primary goal of the hotspots is to cover the most threatened centers of plant diversity, but their efficacy has not yet been tested empirically. For sub-Saharan Africa, our study evaluates the hotspots postulated by Myers and compares them to a set of redefined hotspots proposed on the basis of mapped distribution data for 5985 plant species. The two sets of hotspots overlap by 48%. Our redefined hotspots include 80% of the species and 66% of the range-restricted species of the sub-Saharan flora in areas under high human

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impact, whereas these values are 15% and 11% lower for Myers's hotspots. Despite having equal size and a considerable spatial overlap with Myers's hotspots, our redefined hotspots include further highly threatened centers of plant diversity in the Maputaland Pondoland Region, in Katanga, the East African Afromontane region, the Lower Guinea Region, and the Albertine Rift. Many of these redefined hotspots are poorly protected centers of plant and animal diversity. Their conservation is essential for a comprehensive coverage of Africa's centers of biodiversity.

Key words: Africa, biodiversity, conservation, endemism, Global Strategy for Plant Conservation (GSPC), hotspots, important plant areas.

There are growing concerns about the coinciding spatial patterns of human population density and biodiversity (Cincotta et al., 2000; Myers et al., 2000; Balmford et al., 2001; Luck et al., 2004). In a pioneering study in 1988, Myers identified a global set of hotspots where exceptional concentrations of species with high levels of endemism face exceptional threats of destruction (Myers, 1988). Later updates (Myers, 1990; Myers et al., 2000) played a crucial role in the public perception of the threat to biodiversity and the development of large-scale concepts for setting spatial priorities for in situ conservation, as required by Article 8 of the Convention on Biological Diversity (UNCED, 1992).

Whereas centers of diversity are identified on the basis of biological richness and endemism, the hotspots concept of Myers et al. (2000) combined two criteria: plant diversity and the threats to that diversity. In practice, hotspots were defined as areas with less than 30% intact primary vegetation and with at least 0.5% of the global plant species being endemic to the area.

Myers et al. based their study on two types of information. In addition to expert advice, they used summary information on the number of endemic species occurring in the hotspots. This "inventory-based type" of information (Barthlott et al., 1999; Mutke et al., 2002) was the only available information on the biodiversity for many areas (Myers et al., 2000; Krupnik & Kress, 2003), though the application and the analysis of this data type is limited (Mutke & Barthlott, in press). Indeed, Myers et al. (2000; see also Brooks et al., 2001) mentioned several areas in sub-Saharan Africa for which the available data are insufficient to decide whether or not they represent a hotspot. They also stated that due to the heterogeneous data situation, they had to use the endemism criterion even though it was felt to be "minimalist" (Myers et al., 2000). In addition, information on biodiversity was, and often still is, only available for comparatively large areas delineated by political boundaries. This low spatial resolution limits the accuracy to which centers of diversity can be identified (Krupnik & Kress, 2003).

More than a decade after the first global set of hotspots was published, it has become possible to define hotspots more rigorously and accountably. Diversity can now be calculated from a "taxon-based type" of information (Barthlott et al., 1999; Mutke & Barthlott, in press), consisting of reliable data on the individual distribution areas of a large number of taxa (Williams, 1996; Burgess et al., 1998). New high-resolution socioeconomic data (CIESIN, 2000; Sanderson et al., 2002) have become available. Complex algorithms (Margules & Pressey, 2000) allow a more precise identification of centers of richness and endemism (Lovett et al., 2000; Linder et al., in press) and permit analyses of the degree of potential conflict between conservation and land-use interests (Balmford et al., 2001; Williams et al., 2003; Luck et al., 2004).

Consequently, taxon-based biodiversity information has been used to criticize the global hotspot areas as defined by Myers et al. (2000) for their conceptual background (Jepson & Canney, 2001), for their performance in comparison to other area networks selected on more complex parameters (Williams et al., 1996; Balmford et al., 2001), for their size (Brummit & Lughadha, 2003), and occasionally for their location (Burgess et al., 2002; Krupnik & Kress, 2003). However, to our knowledge, there is no study that assesses whether the hotspots do indeed cover the most threatened centers of plant diversity, even though this was the original intention of this prioritization scheme.

In this paper we evaluate the extent to which Myers's hotspots include a maximum number of rare plant species in those areas most threatened by human impact in Africa. This is important for four reasons: (i) as the foundation of food webs, plants are of essential importance for terrestrial biodiversity; (ii) plants might be the best available surrogate to represent invertebrate diversity (Myers, 1988); (iii) plant diversity is insufficiently covered by current networks of protected areas (Burgess et al., in press); and (iv) plants are the group from which hotspots were identified by Myers et al.

Which criteria should be used to evaluate and enhance the performance of the hotspots? A modification of the current hotspots would be desirable if they exclude areas in which more rare plant spe-

cies are more threatened by human impact than in included areas. Here we test the efficacy of the hotspots using the most comprehensive available database of plant species distributions for sub-Saharan Africa.

Methods

Species Database

Since 2003, an international group of research institutions has contributed data on Africa-wide plant distributions to the *Biogeographic Information System on African Plant Diversity* (*BISAP*), which is hosted and curated by the BIOMAPS Project within the BIOLOG BIOTA framework (www.biota-africa.org).

The database includes Africa-wide distribution records for 6269 species (status March 2004), all of which had been taxonomically revised. The database comprises about 330,000 distribution records from confirmed collection localities. The spatial precision of the data varies from exact localities (mainly from herbarium collections with geo-referenced localities) to one-degree resolution data from digitized maps. Data are organized in MS Access databases and have been plotted and analyzed using WORLDMAP software (Williams, 2002) and ArcView 3.2a GIS software (ESRI, 2000). In order to achieve maximum comparability with previous analyses on sub-Saharan zoodiversity (Balmford et al., 2001; Brooks et al., 2001; Burgess et al., 2002; Burgess et al., in press; Fjeldså et al., 2004; De Klerk et al., 2004), all plant distribution data were rescaled to a one-degree grid resolution within a base map of 1713 one-degree latitude-longitude grid cells covering mainland sub-Saharan Africa south of 17 degrees latitude. By restricting the geographic coverage to Africa south of the Sahara and excluding those species found only on offshore islands, a database with 5985 plant species remains for further analyses. This is between 10% and 15% of the species in the African flora (Lebrun & Stork, 1991–1997; Beentje et al., 1994). Additional information on the origin of this data set is documented in Burgess et al. (in press, see also footnote 1).

Our plant data are the most comprehensive ever assembled for the study area, but inevitably have limitations. There are certain areas in Ethiopia and Somalia, Sudan, the Central African Republic, the Republic of Congo, the Democratic Republic of Congo, and Angola where analysis of sampling intensity indicates that plant diversity is not adequately documented in our databases (W. Küper, unpublished data). The scientific exploration of these areas is an important challenge for the future. Inadequate availability of distribution data could have two effects on our analysis: First, in cases where we have inadequate data for areas included in the hotspots as delineated by Myers et al. (2000), testing the hotspots on the basis of our data might result in an underestimation of their performance in covering sub-Saharan plant diversity. However, in fact the most detailed, updated, and comprehensive distribution data in our database is for those areas covered by the Myers's hotspots (which may partly be a consequence of highlighting these areas since 1988): (i) Data for the upper Guinea (West Africa) hotspot stem from the National Herbarium of the Netherlands–Wageningen branch; (ii) data for the Western Cape are from the National Botanic Institute, Republic of South Africa, and contributed by T. Rebelo and N. Jürgens; and (iii) distribution data for East Africa stem from a compilation of restricted-range species for the area of the Flora of Tropical East Africa (H. Beentje, unpublished data, together with other sources). Even though the data for West Africa are comparatively comprehensive, the eastern part of the upper Guinea hotspot is potentially less well represented due to lower data availability. Second, it is possible that the selection of our alternative set of hotspots on the basis of our data misses areas that are richer in species than those included simply because the former ones are not adequately collected. This is certainly a key problem if areas are selected on the basis of species richness alone. But this problem is not as prominent when selecting hotspots, because their identification is also based on the intensity of human impact. Hotspots tend to be particularly well collected (i) due to their popularity with biologists (Reddy & Dávalos, 2003) and (ii) because their high human impact is associated with a comparatively good infrastructure providing access (Gibbs Russell et al., 1984).

Digitizing the Hotspots of Myers et al.

In order to compare the sub-Saharan hotspots of Myers et al. (2000) with our data arranged in one-degree cells, we first digitized Myers's hotspot polygons (delineations taken from Mittermeier et al., 1999) and overlaid them on our grid of cells. We then identified all cells that had a spatial overlap of more than 25% of their area with the hotspots polygons (see methods in Burgess et al., 2002). The decision to accept or omit cells with less than 25% overlap could affect the performance of the hotspots in covering Africa's most threatened centers of plant diversity compared to alternative hotspots de-

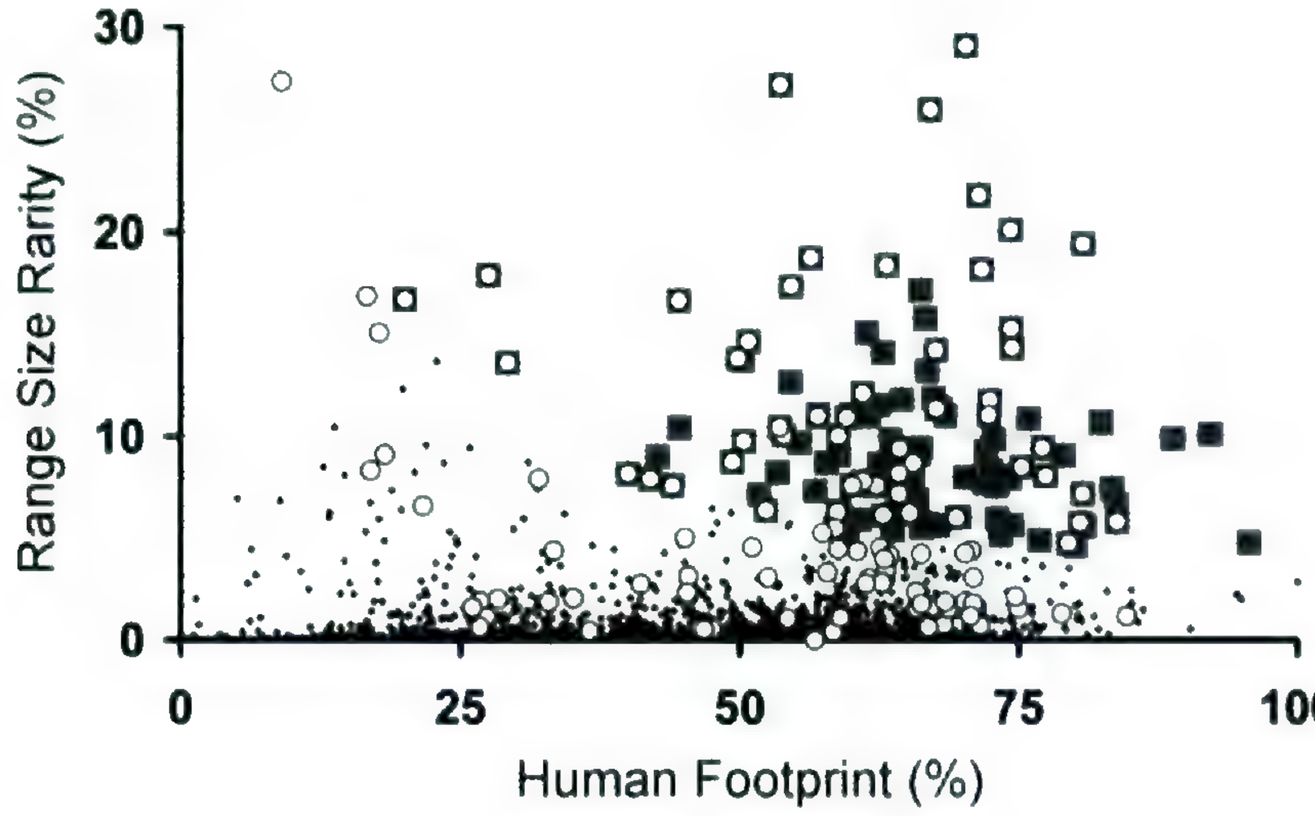

Figure 1. Scatterplot illustrating the values of range-size rarity and mean human footprint (rescaled from Sanderson et al., 2002) for each of the 1713 sub-Saharan one-degree cells (each represented by a black dot, partly concealed by other symbols). Both parameters are rescaled to percentages. For better visualization, the seven cells with a range-size rarity of more than 30% are not shown (X/Y-values for these cells: (63/100), (75/89), (99/68), (97/60), (38/42), (53/36), (42/35)—these are all in both Myers hotspots and redefined hotspots). Open circles: 125 cells covered by the Myers hotspots. Gray boxes: 125 cells with highest product of range-size rarity and human footprint, cited as "redefined hotspots" in the text.

lineated on the basis of our data. We therefore tested whether the inclusion of further cells (those with less than 25% overlap) would improve the performance of the hotspots in comparison to our redefined hotspots of equal area in each case. If this was the case, we accepted the cell as part of the hotspots. With this most conservative method in favor of the performance of the Myers et al. hotspots, 125 cells were identified as being part of these hotspots. From here on, they will be referred to as "Myers hotspots" (Fig. 2A).

CHOOSING DATA TO REPRESENT PLANT ENDEMISM AND ITS THREAT

The aim was to select data to best approximate the two criteria used for the delineation of the Myers hotspots, which were plant endemism and threat. Using our data we selected 125 cells in which plant diversity and threat are maximized (Fig. 1) on the basis of the following two measures. (i) We calculated range-size rarity for each cell (Fig. 2B). This combines the number and range sizes of species in each cell (Williams, 1996; Kier & Barthlott, 2001; Wieringa & Poorter, 2003). The more species that occur in a cell and the smaller their ranges are, the higher the value. We chose range-size rarity since it best approximates the endemism criterion applied by Myers et al. (2000). In contrast to their criterion, range-size rarity includes not only the species strictly endemic to the hotspots, but also every species whose range overlaps with them. Hence, two areas with the same number of strict endemics can still be differentiated according to their contribution in covering the ranges of other species. (ii) As a surrogate for threat, we calculated the mean human footprint for each cell, rescaling the data from Sanderson et al. (2002) to one-degree cells (following the methods used in Balmford et al., 2001; Luck et al., 2004). For coastal cells, the mean footprint was calculated on the basis of mainland values only. The human footprint index shows similar spatial patterns to parameters such as population density, which was used in previous studies (Balmford et al., 2001; Lesslie, 2002; Luck et al., 2004), but in addition takes into consideration a wider range of factors, such as infrastructure and land-cover. Thus, agricultural areas that do not necessarily have a high human population density are included as having a high human impact on biodiversity. We calculated mean values of human

→

Figure 2. —A. Map of the set of redefined hotspots identified in the present study, contrasted with the hotspots as delineated by Myers et al. (2000). Solid black line within continent: *Myers hotspots*. Gray open squares: 125 one-degree grids covered by the Myers hotspots (see methods). Red squares: 125 cells covered by the *redefined hotspots* (cells with highest product of range-size rarity and mean human footprint per cell). Black dots represent 125 first cells (compare Table 1) of a near-minimum-cost area set (Williams, 2002, the entire near-minimum-cost set is illustrated in Fig. 2B). —B. Range-size rarity per one-degree grid cell. This measure combines the values for richness and the range sizes of the species occurring in each cell. It is calculated as the sum of the inverse range sizes per cell (Williams, 1996).

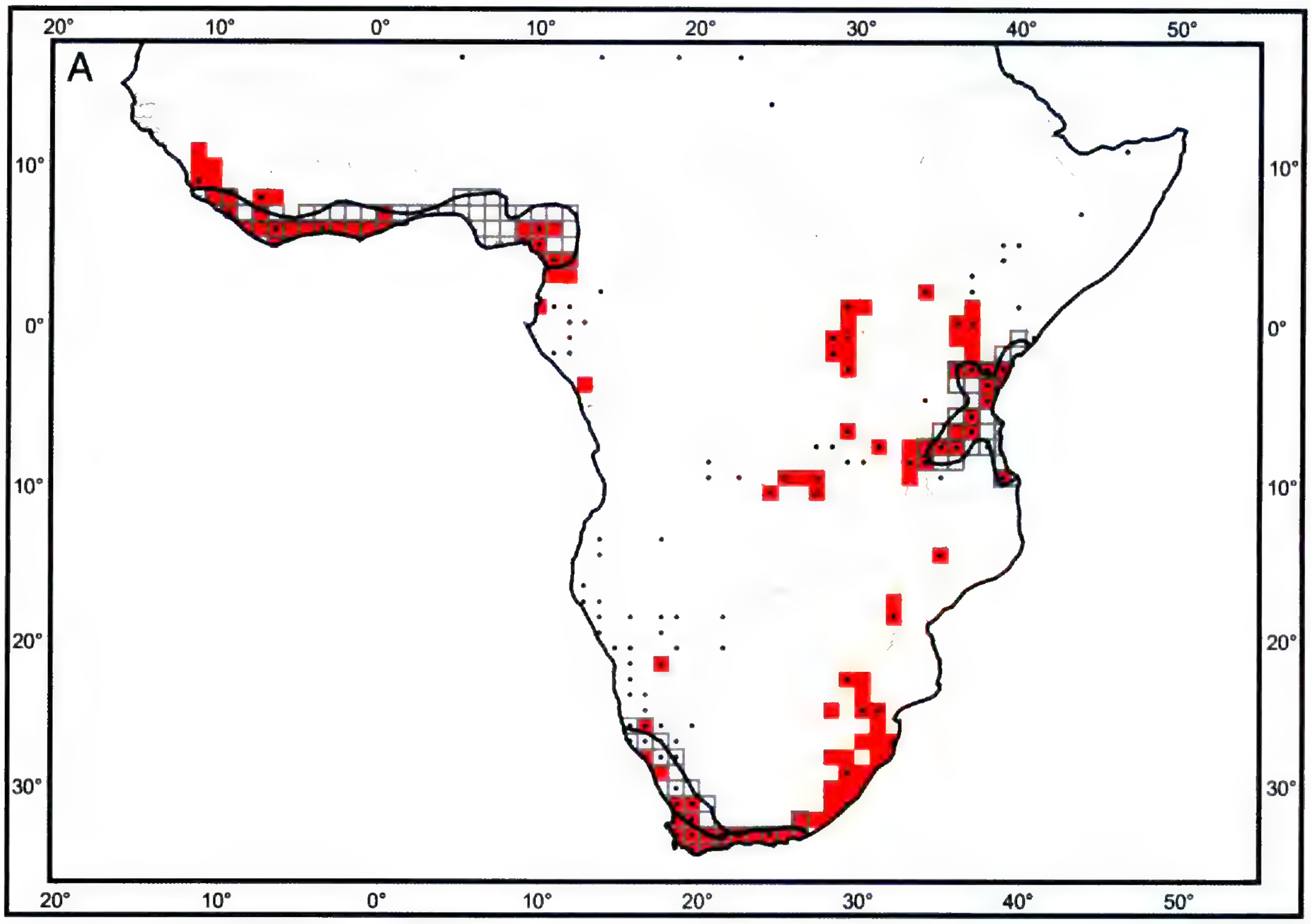

Figure 2. —B. (Continued) Note that many species of medium range size may result in a similar cell value as one with fewer species of very small range size. Black dots mark 422 cells that form the near-minimum-cost area set for sub-Saharan plant diversity in the data set (Williams, 2002). These cells represent all 5985 plant species in a set with near-minimum total human footprint. The figure shows Africa south of 17ºN latitude with grey background lines indicating national boundaries.

footprint per cell so that roads or populated places close to relatively intact areas do not dominate the values for these cells. From here on, mean footprint per cell is referred to as "human footprint."

IDENTIFYING HOTSPOTS ON THE BASIS OF OUR DATA

(i) Range-size rarity and human footprint were normalized to a percentage of their maximum value, so that they are both equally scaled.

(ii) To represent a measure that best approximates the "heat" of the Myers hotspots, we then calculated the product of the value of footprint and range-size rarity. This index, which combines biodiversity and human impact, does not fully reproduce the methods of Myers et al. and is too simplistic to derive any detailed conclusions on conservation priorities. However, it is suitable for representing the degree of potential conflict between the conservation of diversity and pressure on land use resulting from existing human activities (Fig. 1, compare methods used by Balmford et al., 2001; Luck et al., 2004). Using the product ensures that both range-size rarity and human footprint must have comparatively high values to obtain a high combined index value.

(iii) The 1713 sub-Saharan cells were then ranked on the basis of the square-root values of the combined index for each cell.

(iv) The top 125 cells with the highest values were selected. We chose only 125 cells so that their total area approximates to the total area of the Myers hotspots. From here on, the 125 cells selected on the basis of our data will be referred to as "redefined hotspots" (Fig. 2A).

COMPARING THE PERFORMANCE OF THE TWO ALTERNATIVE SETS OF HOTSPOTS

Although the redefined hotspots cover the 125 cells with the highest product of range-size rarity and human footprint, this does not necessarily mean that they must include more rare species in total, or indeed a larger proportion of the species' ranges than do the Myers hotspots. To compare both sets of hotspots, we applied three tests: (i) How many species are included? (ii) How many species belonging to the quartile of species with most-restricted ranges (see Gaston, 1994) are included? (iii) Which proportion of the ranges of the sub-Saharan plant species is covered? The latter measure is calculated by summarizing the values of range-size rarity for all cells included in each set (analogous to the C-value of Kier & Barthlott, 2001). From here on this measure is referred to as "cumulative range-size rarity." The parameters tested were considered to be the best measure of any set of areas to fulfill the original aims of the Myers hotspots.

HOTSPOTS AS CONSERVATION PRIORITIES?

The Myers hotspots are promoted as a network of areas suitable to "protect the most species per dollar invested" (Myers et al., 2000). This resembles the goal of recently applied heuristic selection algorithms for seeking near-minimum-cost area sets (Gaston, 1994). The latter type of area sets represents each species at least once, but tends to minimize the hypothetical "costs" of potential conservation actions by choosing cells with, for example, least human impact (Balmford et al., 2001; Williams et al., 2003), or at least cost (Moore et al., 2004). The approach aims to alleviate conservation conflicts where there is scope for this (Luck et al., 2004). Technically, the algorithm for near-minimum-cost area set counts the number of rare species in each cell (after taking floristic complementarity with previously chosen cells into account) and then divides the diversity score for each cell by the human footprint value of the respective cell. Such a near-minimum-cost area set was calculated on the basis of the same parameters used for the hotspots analyses. We then selected the 125 cells having the highest benefit-to-cost ratio and contrasted them with the Myers hotspots and the redefined hotspots (Table 1, Fig. 2A, B).

RESULTS

There is a substantial spatial overlap (Figs. 1, 2) between the Myers hotspots and the redefined hotspots identified on the basis of our data. The top 17 redefined hotspot cells are included in the Myers hotspots as well. A total of 60 out of the 125 cells covered by the Myers hotspots are also identified as redefined hotspots.

The 125 cells in the Myers hotspots include 3841 of the 5985 sub-Saharan plant species represented in our database (Table 1). Fifty-two percent of the species belonging to the quartile of species with most restricted ranges are included. Cumulative range-size rarity for all cells is very high, with 39% of the maximum cumulative value for all 1713 sub-Saharan cells. The average human footprint among the 125 cells is 24.32; similar values are measured in cells covering cities such as Kigali, Kisangani, or Bloemfontein. Values higher than 30 are characteristic of metropolitan areas such as Durban, Cape Town, Dar es Salaam, Abidjan, and Douala.

Table 1. Comparative performances of three area sets of equal size to cover the sub-Saharan centers of plant diversity. The following sets are compared: the hotspots as defined by Myers et al. (2000), a redefined set of hotspots identified on the basis of distribution data for 5985 plant species, and a near-minimum-cost area set on the basis of the same data. In order to compare the sets, all have been rescaled to a one-degree based grid of 1713 cells covering Africa south of 17°N latitude. The comparison is based on four criteria: (i) overall number of species covered; (ii) number of restricted range species covered; (iii) cumulative range-size rarity for the included cells; and (iv) human footprint (sum and average for the included cells). Percentages indicate the proportion of the respective total values for sub-Saharan Africa. The plant data stem from the Biogeographic Information System on African Plant Diversity (BISAP) representing 10%–15% of the species of the sub-Saharan African flora. Note that the aim of hotspot sets is to cover the most threatened centers of plant diversity (represented by high values for both plant diversity and human footprint), whereas the near-minimum-cost area set seeks to cover all species in cells with a human footprint as low as possible.

	Sub-Saharan Africa	Myers Hotspots		Redefined Hotspots		Near-minimum-cost set	
	Total	Total	%	Total	%	Total	%
One-degree cells	1,713	125	7.3	125	7.3	125	7.3
All species	5,985	3,841	64.2	4,759	79.5	5,196	86.8
Restricted-range species	1,540	802	52.1	1,011	65.6	1,155	75
Range-size rarity (sum)	5,985	2,354	39.3	2,955	49.4	2,603	43.5
Human footprint (sum)	33,965	3,040	—	3,420	—	2,215	—
Human footprint (average)	19.8	24.3	—	27.4	—	17.7	—

However, the Myers hotspots exclude some of the cells with very high range-size rarity and human footprint, and conversely include other cells with comparatively low values for range-size rarity and human footprint (Figs. 1, 2). In total, 65 cells of the redefined hotspots do not coincide with the Myers hotspots (see below).

In an area of approximately the same size as the Myers hotspots, the redefined hotspots include 15% more of all species and 11% more of the rare species occurring in our databases for sub-Saharan Africa (Table 1); in total, that is about 80% of the species included in our databases. Moreover, they cover a 25.5% higher cumulative range-size rarity than the Myers hotspots—and they do so in areas that are characterized by a 12.5% higher total human footprint.

The redefined hotspots overlap with regional centers of plant diversity not covered by the Myers hotspots (Fig. 2A, B). In southern Africa these are mainly cells in Maputaland, Pondoland, Barberton, Sekhukhuneland, and Soutpansberg. In Katanga, the Zambezi Source Area, Kundelungu and Upemba National Park are important. In eastern Africa, the Chimanimani Centre, Mt. Mulanje, a large block of cells in the Albertine Rift including the Kivu area, the Ruwenzori and Virunga Volcanoes, Bwindi forest, Mt. Elgon, Mt. Kenya, as well as other areas with Afromontane or Afroalpine vegetation mainly in Kenya are among the redefined hotspots (Fig. 2). The same is true for cells in the lower Guinea forest block, including parts of southeastern Cameroon and the area between Crystal Mts. and the coast in Gabon, the Mayombe center of plant diversity. These areas have been identified as centers of plant diversity before (for example, in Brenan, 1978; Beentje et al., 1994; Olson & Dinerstein, 1998; van Wyk & Smith, 2001).

The 125 cells selected for the near-minimum-cost area set for sub-Saharan plant diversity have an overlap of 58 cells with the redefined hotspots (Fig. 2). The overlap is high because all regional clusters of redefined hotspots contain cells with one-cell endemics. Although the algorithm seeks to avoid hotspots and instead chose alternative cells with a low human impact, this is not possible for many cells because they are irreplaceable for representation of their endemic species. Even though the redefined hotspots have been delineated on the basis of simplistic criteria and methods, the irreplaceability of a considerable part of their area implies that they will play an important role in more complex and more adequate prioritizing schemes—there are simply no alternatives in many cases.

However, the top 125 cells of the near-minimum-cost area set include more species and more restricted-range species than the Myers hotspots and the redefined hotspots, even though they include a set of cells with a much smaller total and average human footprint. Bearing in mind the limited comparability and simplified assumptions of the algorithm, this result indicates that, instead of prioritizing all hotspots as "conservation areas," there is potential to alleviate conservation conflicts in sub-Saharan Africa by prioritizing areas with less hu-

man impact for conservation, such as, for example, a rainforest block in central Gabon (see Fig. 2).

Discussion

A redefined set of sub-Saharan hotspots

The Myers hotspots cover 64% of all plant species and more than half of the restricted-range plant species included in our database for sub-Saharan Africa.

Although this is an impressive performance for only 125 cells (7.3% of the total area), the redefined hotspots have an even higher representation of the threatened sub-Saharan flora (Table 1). This is mainly due to the fact that some important centers of plant diversity under high human impact are not included in the Myers hotspots.

Several of these areas have been mentioned by Myers et al. (2000), but their inclusion in the Myers hotspots was uncertain due to poor data availability. These data are now available and strongly support inclusion (see also Brooks et al., 2002). Moreover, some of the sites have been identified as major gaps in the network of protected areas (IUCN categories I–VI plus forest reserves) for threatened and restricted-range Afrotropical plants (Burgess et al., in press). This emphasizes the urgency to consider them in large-scale conservation assessments.

In the Myers hotspots analysis zoological diversity served as "backup support" (Myers et al., 2000). Patterns of plant and zoological diversity are not necessarily congruent. There are, for example, obvious differences in the importance of the Western Cape or Kaokoveld in the diversity of restricted-range plants compared to birds or mammals. Nonetheless, the majority of cells now included in the redefined hotspots are centers of species richness and endemism for animals as well. This is true for the Albertine Rift (Plumptre et al., 2003) including the Kivu area, the southwestern connection of the Eastern Arc to the Mbeya Range, nearly all of the Afromontane areas mentioned above, including Mt. Elgon, Mt. Kenya, and the Chimanimani Mts., some of the areas in northeastern Southern Africa and also Katanga (Burgess et al., 2004; Cotterill, in press). Range-size rarity patterns for mammals, snakes, and amphibians (Brooks et al., 2001) are very similar. In analyses that are currently most comprehensive for sub-Saharan zoological diversity, many of these areas have been classified as irreplaceable in the context of biodiversity conservation (Balmford et al., 2001) but are inadequately protected (De Klerk et al., 2004; Fjeldså et al., 2004; Burgess et al., in press; Rodrigues et al., 2004). If we want to base hotspots on this list of taxa, many of the newly redefined hotspots would certainly have an equal priority in comparison to the areas currently included in the Myers hotspots.

The most obvious difference between the Myers hotspots and the redefined hotspots is their spatial resolution, in particular for the Afrotropical region. The distribution of the species within the Myers hotspots was not known, but in our study it was possible to optimize the performance of the redefined hotspots on a spatial scale of one degree. Hence, several cells within the hotspots have been replaced by others previously not considered.

The low resolution of inventory-based data limits not only the spatial precision of the identification of centers of diversity, but also their comparability. The Myers hotspots by definition have to include at least 1500 endemic species per hotspot. This does not take into account the fact that some areas with high regional concentrations of restricted-range species, such as the Albertine Rift, cannot match this threshold because they are too small (Plumptre et al., 2003). Since the distribution of the endemics within the Myers hotspots was not known in many cases, priority of hotspots was determined by ranking the average number of endemics per standard area. In contrast, taxon-based distribution data can be used to compare any of the 1713 sub-Saharan one-degree cells enabling comparison of areas such as the central part of the Albertine Rift or the Maputaland Center of plant endemism with parts (not the average) of the hotspots in West Africa. In addition, instead of only considering the number of endemics and the threat per area, taxon-based data can provide a variety of additional parameters, such as diversity at higher taxonomic level or even phylogenetic diversity, enabling creation of a hierarchy of priorities.

Toward a network of priority areas for conservation

The Myers hotspots had a very important impact as a pioneering study demarcating areas where ongoing "mass extinctions" (Myers, 1990) make it most urgent to conserve biodiversity. In parallel, they have been promoted also as a network of areas suitable to "protect the most species per dollar invested" (Myers et al., 2000). At first glance this seems to be contradictory since the most problematic areas for conservation are unlikely to be those where conservation is most cost-effective. However, our results indicate that there are indeed often no alternatives to protection of narrowly endemic species within centers of human settlement and intensive land use. The 125 cells identified as redefined

hotspots are inhabited by more than 80 million people (population data according to [RWPE], 2002) and the vast majority of the areas of high plant endemism in sub-Saharan Africa are characterized by a very high human footprint (Fig. 1). Despite their vicinity to metropolitan areas such as Cape Town, Abidjan, Douala, and Dar es Salaam, and despite being often completely surrounded by converted land, many sites of "remaining primary vegetation" (Myers et al., 2000) within hotspots (such as, for example, Taï and Banco National Park of Côte D'Ivoire, Table Mountain National Park of the Republic of South Africa, and the Coastal Forests of eastern Africa) are irreplaceable due to the many restricted range species they contain. Due to this irreplaceability, a large proportion of the areas delineated in the Myers hotspots cannot be substituted for other areas, even if the latter had an even higher plant species richness. In our study, the redefined hotspots were constrained by being the same spatial size as the Myers hotspots. Consequently, the inclusion of new areas formerly not considered in Myers hotspots resulted in omitting others previously included. Moreover, a range of additional areas could not be included despite having considerable numbers of restricted-range species and despite being highly threatened. For effective conservation, inclusion of all areas containing clusters of strict endemics is a minimum requirement. For example, the Namib desert and arid woodlands of northeastern Somalia are also key areas for plant conservation. Moreover, in order to translate the hotspots concept to conservation in the field, floristic checklists of areas with comparatively intact vegetation and, in particular, checklists of existing protected areas are needed in order to quantify how many restricted-range taxa are already protected so that conservation gaps can be determined. This will help African countries comply with international agreements such as the Global Strategy for Plant Conservation (GSPC), which requires signatories of the Convention on Biological Diversity to assure protection of 50% of the most important plant areas by the year 2010 (Lovett, in press).

Although many irreplaceable parts of sub-Saharan hotspots are in sites of high pressure for alternative land uses, there are also areas with high range-size rarity and a comparatively low human impact (Fig. 1). These areas could contribute to optimizing conservation efficiency and alleviating conservation conflicts. However, the data on which the Myers hotspots and the extremely broadly defined "high biodiversity wilderness" (Mittermeier et al., 2003) areas are based do not account for complementarity and hence cannot be used to generate priorities on the basis of cost-effectiveness. To meet targets of initiatives such as the GSPC, taxon-based data are the key information. This includes information on species distributions in areas that have so far remained comparatively untransformed because of difficult access—and that tend to be undercollected for the same reason. For example, how many species in the heavily transformed hotspot around Monrovia could be efficiently protected in the largely underexplored Krahn Bassa National Forest or Sapo National Park in southeastern Liberia? Similarly, we do not yet know the potential of the undercollected border triangle of Cameroon, the Republic of Congo, and the Central African Republic for the conservation of the lower Guinea rain forest and its ecotones.

PRIORITIES FOR A GLOBAL CONSERVATION STRATEGY

We see three priorities for the future application of taxon-based data in the context of biodiversity conservation. The first priority must be to acquire these data at a finer spatial resolution. If the current progress of data acquisition continues, it is likely that before 2010 reliable distribution data for plants will be available at a quarter-degree resolution for the majority of the globally most biodiverse ecoregions, a scale which approaches that at which actual conservation actions are implemented. In particular, in addition to further exploration of the hotspots, we urgently need better information on the biodiversity of remote areas with intact vegetation and of existing protected areas. A second priority is to combine botanical and zoological information to obtain a clear picture of overall biodiversity. There is some preliminary evidence of concordant centers of endemism among many different taxa particularly in geodiverse areas such as Afrotropical mountains, and these areas should have a high priority for conservation action. Third, the high resolution biological data need to be compared with socioeconomic information and remote sensing data on habitat status. Inevitably, biodiversity in large parts of the redefined hotspots has already been drastically reduced. The combination of remote sensing and taxon-based biodiversity data, therefore, seems to be a promising avenue leading to identification of those sites where we can protect biodiversity in an efficient and sustainable way.

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Internet Resources

[RWPE] United Nations. 2002. Revision of the World Population Estimates and Projections. ⟨http://www.unpopulation.org⟩

[BIOTA] Biota Project. ⟨www.biota-africa.org⟩

A REVISION OF THE MASCARENE SPECIES OF *ELAPHOGLOSSUM* (ELAPHOGLOSSACEAE)[1]

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ABSTRACT

A taxonomic revision of *Elaphoglossum* in the Mascarene Islands (southwest Indian Ocean) is presented here based on a treatment written for the *Flore des Mascareignes*. Seventeen species are recognized for the islands of Mauritius and Réunion. Of these species, seven are endemic. The non-endemic species also occur in Madagascar, Africa, or the Paleotropics in general. In addition, five natural interspecific hybrids (nothospecies) occur in the Mascarenes. Two lectotypes are designated for the name *Acrostichum inversum* and are referred *pro parte* to *E. acrostichoides* and *E. angulatum*.

RÉSUMÉ

Une révision taxinomique d'*Elaphoglossum* des îles Mascareignes (sud-ouest de l'Océan Indien) est présentée ici, fondée sur un traitement écrit pour la *Flore des Mascareignes*. Dix-sept espèces dont sept endémiques sont reconnues pour les îles de Maurice et de La Réunion. Les espèces non-endémiques se trouvent également à Madagascar, en Afrique, ou dans les Paléotropiques en général. De plus, cinq hybrides interspécifiques naturels (notho-espèce) sont présents dans les Mascareignes. Deux lectotypes sont désignés pour le nom *Acrostichum inversum* et sont attribués *pro parte* à *E. acrostichoides* and *E. angulatum*.

Key words: Elaphoglossaceae, *Elaphoglossum*, hybrids, Mascarene Islands, Mauritius, nothospecies, pteridophytes, Réunion, southwest Indian Ocean.

The Mascarenes are a trio of volcanic oceanic islands situated in the southwest Indian Ocean. Approximate sizes and ages (millions of years) of the islands are: Réunion, 2500 km², 3.0 MA; Mauritius, 1865 km², 7.8 MA; and Rodrigues, 110 km², 1.5 MA (Fisher et al., 1967; McDougall & Chamalaun, 1969; McDougall et al., 1965). The mean annual precipitation ranges from 1000 to 6000 mm in Mauritius and Réunion and from 1100 to 1700 mm in Rodrigues. The rainy, austral summer season punctuated by occasional tropical cyclones lasts from December to April, and the relatively drier and cooler winter season lasts from May to November (Lorence, 1985). Except in coastal areas with coral sand, Mascarene soils are derived from decomposed basaltic lavas.

Relative to their small surface area the Mascarenes possess a diverse pteridophyte flora, with 273 species comprising 282 taxa including infraspecies (Badré & Cadet, 1978; Lorence, 1976b, 1978, 1992). Of these, 265 species are indigenous and 8 are adventive or naturalized. Of the indigenous species, 22.7% are endemic to the Mascarene archipelago or to a single island.

Among the most species-rich fern genera on the island is *Elaphoglossum* Schott ex J. Sm., a large

[1] Use of facilities and financial assistance provided by the Mauritius Sugar Industry Research Institute at Réduit, Mauritius, are gratefully acknowledged while the first author served as a U.S. Peace Corps Volunteer at the Mauritius Herbarium (MAU). A portion of the fieldwork by the second author was supported by the "PPF Populations fractionnées et insulaires de l'Ecole Pratique des Hautes Etudes." We thank the curators of the following herbaria for making their specimens available for study: B, BM, K, MAU, MO, MPU, P, PR, PRC, PTBG, and REU. Frédéric Badré (P) provided encouragement and reviewed an earlier version of the manuscript. We are grateful to Brigitte Zimmer (B) for providing digital images of the collections in the Willdenow Herbarium (B-W) and for helpful suggestions and comments. We thank Victoria Hollowell, John Mickel, Robbin Moran, and Henk van der Werff whose comments and reviews greatly improved the quality of the paper.

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and taxonomically complex pantropical genus. Worldwide, the genus comprises about 600 species of primarily epiphytic, lithophytic, and casually terrestrial ferns concentrated in tropical wet forests and cloud forests (Mabberley, 1997; Mickel & Atehortúa, 1980; Mickel & Beitel, 1988). Although the greatest species diversity occurs in the Andes of South America, *Elaphoglossum* has undergone slight adaptive radiation in a number of oceanic islands and archipelagos such as Hawaii with 9 species (Palmer, 2003) and the Mascarene Islands with 17 species (Lorence, 1978, 1984). In the Mascarenes, *Elaphoglossum* occurs only on the two largest and highest islands, Mauritius and Réunion: it is absent from the smaller and drier Rodrigues Island (Lorence, 1976b). Of the 17 Mascarene species, 7 are endemic and 10 occur elsewhere primarily in Madagascar, the Comoro Islands, Africa, or the Paleotropics in general. In addition to these 17 species, five natural hybrids (nothospecies) are known, indicating the genus is in an active state of evolution in the Mascarenes (Lorence, 1984).

The following revision of *Elaphoglossum* is based on a treatment of Lomariopsidaceae s.l. originally written in French for the *Flore des Mascareignes*, a joint collaborative project between the Royal Botanic Gardens Kew, the Mauritius Herbarium at the Mauritius Sugar Industry Research Institute, and Institut de Recherche pour le Développement (IRD, formerly ORSTOM) based at the Paris Muséum National d'Histoire Naturelle. Because publication of the pteridophyte fascicles for this project has not yet taken place, we decided to publish this revision to make the information available in a timely manner. In addition, we provide supplemental habit photos and drawings of rhizome scales to facilitate identification.

Materials and Methods

This taxonomic revision is based on 717 herbarium specimens and field observations of all the *Elaphoglossum* species occurring in the Mascarenes. All measurements given in the descriptions have been taken from dried herbarium specimens. Unacetolized spores were mounted in glycerine jelly, and their size measurements were taken excluding the perispore. Secondary or lateral veins that are apically free versus united provide an important, species-specific character, but the fronds must be held up to a bright light or, in some cases, chemically cleared to see the venation. Collections with morphological characters intermediate between two species that occur in the same vicinity and have a high percentage of aborted spores (features such as collapsed, irregular spore shape and size) are suggestive of hybrid origin as already documented for other pteridophyte genera (Wagner & Chen, 1965; Wagner et al., 1986). Nevertheless, aborted spores alone are not an absolute criterion of hybridism because there are several other possible sources of abortion such as the metabolic conditions of the plant, which may be influenced by cold or drought shocks during spore development (Hennipman, 1977).

Taxonomic History

The name *Elaphoglossum* was first published, without description, by Schott (1834), and was not validated until Smith (1841) attributed the name to Schott and published a description and cited a type species. Morton (1965) proposed *Elaphoglossum* Schott ex J. Sm. as a conserved generic name against *Peltapteris* Link, which was also published in 1841.

Elaphoglossum is characterized by its dimorphic fronds with acrostichoid sori (in addition, nearly all the species have an elongated ventral meristele in the rhizome, simple and entire laminae, and free veins). Because of its soral condition, many species of *Elaphoglossum* were originally described under *Acrostichum* L. (e.g., Bojer, 1837; Fée, 1845; Baker, 1877; Cordemoy, 1895). This proved to be a polyphyletic grouping, as the type species *Acrostichum aureum* L., which also has acrostichoid sori, belongs to the Pteridaceae (e.g., Tryon & Tryon, 1982). Most taxa of *Elaphoglossum* originally described in *Acrostichum* were subsequently transferred to *Elaphoglossum*, or to *Aconiopteris* C. Presl or *Hymenodium* Fée (now both considered synonyms of *Elaphoglossum*). Most of these transfers were made by Moore (1857–1862).

The difficulties in establishing phylogenetic relationships of *Elaphoglossum* to other ferns may explain why in modern times the genus has been taxonomically treated along diverse lines, namely: (1) as a part of the family of Lomariopsidaceae Alston (Alston, 1956; Kramer et al., 1990; Moran & Riba, 1995), which is the concept retained within African literature (e.g., Alston, 1959; Tardieu-Blot, 1959, 1960; Schelpe, 1969; Roux, 2001; Mickel, 2002); (2) as a member of the family Elaphoglossaceae described by Pichi Sermolli (1968); (3) as a member of a subfamily: Aspleniaceae Mett. ex A. B. Frank subfam. Elaphoglossoideae (Pic. Serm.) Crabbe, Jermy & Mickel (Crabbe et al., 1975); and (4) as a member of the tribe Bolbitideae Pic. Serm. included in the family Dryopteridaceae Herter (Tryon & Tryon, 1982).

The most recent comprehensive systematic account of the genus as a whole is the *Monographie des Genus Elaphoglossum* (Christ, 1899). This treatment covered 134 species and detailed 32 taxonomic groups. More recently Mickel and Atehortúa (1980: 47) subdivided the genus into sections and subsections, but they emphasized that "this treatment is provisional because a complete understanding of the genus can be had only after the species are better known." Even with the first phylogenetic studies of the genus (Rouhan et al., 2004), knowledge of the systematics and phylogeny of *Elaphoglossum* is far from complete, and new species continue to be described. The present paper aims at providing new knowledge and a modern taxonomic treatment of the genus in the Mascarene region.

Taxonomic Treatment

Elaphoglossum Schott ex J. Sm., J. Bot. (Hook.) 4(27): 148. Aug. 1841, nom. et typ. cons. TYPE: *Elaphoglossum conforme* (Sw.) J. Sm., J. Bot. (Hook.) 4(27): 148. 1841 [*Acrostichum conforme* Sw., Syn. Fil. (Sw.) 10, 192. 1806].

Hymenodium Fée, Mém. Foug., 2: 20. 1844 [1845]. TYPE: *Hymenodium crinitum* (L.) Fée, Mém. Foug., 2: 90. 1844 [1845] [*Acrostichum crinitum* L., Sp. Pl. 2: 1068. 1753].

Peltapteris Link, Fil. Spec. 147. 1841. TYPE: *Peltapteris peltata* (Sw.) C. V. Morton, Amer. Fern J. 45: 13. 1955 [*Osmunda peltata* Sw., Prodr. 127. 1788].

Microstaphyla C. Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 520–521. 1851. TYPE: *Microstaphyla bifurcata* (Jacq.) C. Presl, Epimel. Bot. 161. 1849 [*Osmunda bifurcata* Jacq., Collectanea 3: 282, tab. 20(4). 1789].

The following discussion clarifies the nomenclature and the typification of the genus *Elaphoglossum*. H. W. Schott was the first to propose the name *Elaphoglossum* (Gen. Fil.: 30, tab. 13. 1834), but this name lacks a description and consequently was not validly published. Validly publishing *Elaphoglossum*, J. Smith attributed the name to Schott (J. Bot. 4(27): 148. 1841) and referred six species to the genus, but he did not select one of them as the type. In a subsequent publication (Hist. Fil.: 125. 1875), J. Smith clearly chose *E. conforme* as the type. Since the date of publication of *Elaphoglossum* is 1841 and not 1834, *Aconiopteris*, which was validly published in 1836, should have priority over *Elaphoglossum* when these genera are united. In order to avoid replacing the well-known generic name *Elaphoglossum* by *Aconiopteris*, the name *Elaphoglossum* and its type *E. conforme* (Sw.) J. Sm. are conserved respectively as *nomina conservanda* and *typus conservandus* (ICBN, App. IIIA; Voss et al., 1983: 296) against *Aconiopteris*, which is based on a type different from that of the conserved name *Elaphoglossum* (Art. 14.4) as follows: *Aconiopteris* C. Presl. [Tent. Pterid.] in Abh. Königl. Böhm. Ges. Wiss., ser. 4, 5: 236, tab. 10(17). 1836 (ante 2 Dec.). TYPE: *Aconiopteris subdiaphana* (Hook. & Grev.) C. Presl, Tent. Pterid. 236, tab. 10(17). 1836 [*Acrostichum subdiaphanum* Hook. & Grev., Icon. Filic. 2, tab. 205. 1831].

Small to medium-sized epiphytic, epilithic, or occasionally terrestrial ferns; rhizome short- to long-creeping, branching or not, dictyostelic, dorsiventral or radial, fronds in 2 or 3 to 5 ranks (Mascarene species), paleaceous, scales basifixed. Fronds simple (all Mascarene taxa), very rarely flabellately lobed, with stipe jointed and swollen into a persistent, dark phyllopodium bearing small lateral aerenchymatous outgrowths when young; blade simple, entire, usually erect but sometimes pendent, chartaceous to coriaceous, glabrate to densely paleaceous, scales often deciduous; secondary (lateral) venation pinnate, simple or dichotomous, tips apically free and thickened or uniting into a submarginal vein or commissure, rarely branching and anastomosing reticulately (not in Mascarene taxa), margin often revolute. Fertile frond similar in shape to sterile, but blade usually smaller and longer stiped; sporangia densely covering abaxial surface of blade except along costa and margin. Spores monolete, bilateral, elliptic to reniform, exine smooth, perispore granular to spiny forming folds or crests. Gametophyte subcordate or ribbon-like, margins undulate or crisped and bearing unicellular hairs with waxy tips, rhizoids reddish brown. Chromosome number $x = 41$ (Manton & Sledge, 1954).

The generic name *Elaphoglossum* refers to the tongue-like shape of the laminae (from the Greek words *elaphos* = stag, and *glossa* = tongue).

In the Mascarene Islands most species grow as low to high epiphytes or are casually terrestrial in moist and wet forests and ericoid (heath) formations. Where conditions are satisfactory, the plants usually root in mats of bryophytes on trees, at bases of shrubs and trees, or on mossy logs or boulders. One species, *E. lanatum*, is restricted to soil or rock of shady stream banks and cliff faces, and *E. spatulatum* grows specifically on large boulders in stream beds.

The Mascarenes harbor seven endemic *Elaphoglossum* species. This suggests the genus is actively evolving in this archipelago (Lorence, 1984), especially given the relatively recent emergence of these islands. Furthermore, five natural

hybrids occur in the Mascarenes (see Lorence, 1984, for detailed discussion concerning the implications of the occurrence of these hybrids in the Mascarenes).

KEY TO THE MASCARENE SPECIES OF *ELAPHOGLOSSUM*

1a. Sterile blades glabrous or bearing (at least when young) rare to scattered, minute, appressed scales 0.5 mm or less long with margins bearing short multicellular hairs with bulbous, glandular tips.
2a. Sterile blades broadly elliptic to ovate, usually 3 cm wide or broader.
3a. Rhizome scales, filiform or bristle-like, dark reddish brown or black.
4a. Rhizome scales 3–5 mm long, stiff, shiny, black; veins in part apically free and in part uniting intramarginally at tips ..... 14. *E.* ×*revaughanii*
4b. Rhizome scales 8–20 mm long, flexible, dull, brown to black; veins uniting apically into a submarginal commissure ..... 18. *E. sieberi*
3b. Rhizome scales broadly ovate to lanceolate, pale orange-brown or tan.
5a. Rhizome scales broadly ovate, the base auriculate with overlapping lobes; rhizome long-creeping ..... 3. *E. angulatum*
5b. Rhizome scales narrowly ovate to oblong, lacking overlapping basal lobes; rhizome short-creeping.
6a. Rhizome scales 4–10 mm long, 1–1.5 mm wide, curling, with margins involute and bearing long, gland-tipped projections, these more numerous toward the base; veins free at tips ..... 12. *E. lepervanchei*
6b. Rhizome scales (10–)15–25 mm long, 2–3 mm wide, flat, with margins entire or bearing rare short projections; veins uniting apically into submarginal commissure ..... 13. *E. macropodium*
2b. Sterile blades narrowly elliptic, oblong or linear, usually less than 3 cm wide.
7a. Surfaces of sterile blade bearing scattered, persistent, light brown resinous punctations (seen under magnification, but not visible on all adult specimens); veins uniting apically into a submarginal commissure ..... 15. *E. richardii*
7b. Surfaces of sterile blade lacking resinous punctations; veins free apically.
8a. Rhizome scales thick, dark brown to black, opaque except paler basally.
9a. Sterile frond with blade at least 15 cm long ..... 6. *E. coursii*
9b. Sterile frond with blade 6–14 cm long ..... 5. *E.* ×*cadetii*
8b. Rhizome scales thin, papery, pale to medium brown, translucent or sometimes opaque apically.
10a. Rhizome scales with darker bands toward apex ..... 1. *E. acrostichoides*
10b. Rhizome scales uniformly pale golden or reddish brown.
11a. Rhizome long-creeping, often branching; fronds spaced 1.5 cm or more apart; rhizome scales flat, broadly ovate, entire ..... 3. *E. angulatum*
11b. Rhizome short- to moderately long-creeping, rarely branched; fronds spaced 1.2 cm or less apart; rhizome scales crisped, involute, narrowly ovate to linear-oblong, margins ciliate especially basally ..... 12. *E. lepervanchei*
1b. Sterile blades bearing (at least when young) on both surfaces and/or the margins numerous conspicuous scales, either subulate, laminate, peltate, or substellate.
12a. Scales of sterile frond stellate or substellate, with 4 to 8 straight hair teeth ..... 11. *E. lancifolium*
12b. Scales of sterile blade basifixed or peltate, or subulate.
13a. Scales of sterile blade subulate, margins entire or occasionally minutely ciliate apically.
14a. Scales of sterile blade dark brown, confined to margins and costa ..... 9. *E. hybridum*
14b. Scales of sterile blade pale brown to reddish brown, scattered over both surfaces of the blade.
15a. Sterile blades linear, thinly chartaceous and translucent, veins readily visible when held up to light ..... 4. *E. aubertii*
15b. Sterile blades elliptic, narrowly obovate, or spatulate, thickly chartaceous, veins not visible when held up to light.
16a. Sterile blades spatulate to narrowly obovate, 1.5–5.5 × 0.5–1.2 cm, apex obtuse ..... 19. *E. spatulatum*
16b. Sterile blades elliptic, 7–10 × 1.5–2 cm, apex acute ..... 17. *E.* ×*setaceum*
13b. Scales of sterile blade peltate or basifixed with flat central portion, the margins fimbriate or strongly ciliate.
17a. Scales of sterile blade closely appressed, suborbicular, scarious, densely fimbriate; rhizome scales with margins scarious or fimbriate.
18a. Rhizome scales 2–3 mm long, claw-like, opaque, dull brown with fimbriate margins; sterile blade with veins all uniting apically into a submarginal commissure ..... 22. *E. tomentosum*
18b. Rhizome scales 6–12 mm long, ovate-oblong with long, bristle-like apex, shiny castaneous to black with pale scarious margins; sterile blade with veins free (some uniting apically in *E.* ×*heterophlebium*).

19a. Sterile blade with veins free apically with thickened tips; rhizome scales black with scarious transparent margins ..... 7. *E. heterolepis*

19b. Sterile blade with veins uniting apically into submarginal loops, those toward base and apex of blade free with thickened tips; rhizome scales castaneous with sparsely dentate or glandular-ciliate margins ..... 8. *E.* ×*heterophlebium*

17b. Scales of sterile blade spreading, toothed with usually paired hair teeth; rhizome scales with margins bearing (at least basally) short hair teeth or sessile glands.

20a. Sterile blades paleaceous only on adaxial surface, rarely a few scales present on abaxial surface along costa ..... 21. *E. stipitatum*

20b. Sterile blades paleaceous on both surfaces, at least when young.

21a. Fronds 2-ranked on rhizome, not densely caespitose; sterile blade covered when young with densely matted scales bearing long, tangled marginal cilia, the scales soon deciduous.

22a. Scales on adaxial surface of sterile blade forming a loose tomentum ..... 10. *E. lanatum*

22b. Scales on adaxial surface of sterile blade closely appressed forming a thin tomentum ..... 2. *E.* ×*adulterinum*

21b. Fronds 2- to 5-ranked on rhizome, usually densely caespitose; sterile blade with persistent scales bearing stiff, marginal long hair teeth.

23a. Sterile blade with both surfaces obscured by a layer of reddish brown scales, with dark brown to black scales often present along abaxial surface of costa ..... 20. *E. splendens*

23b. Sterile blade with both surfaces visible, covered with loose, pale reddish brown scales along the veins ..... 16. *E. rufidulum*

1. Elaphoglossum acrostichoides (Hook. & Grev.) Schelpe, J. S. African Bot. 30: 196. 1964. *Vittaria acrostichoides* Hook. & Grev., Icon. Filic. 2: tab. 186. 1830. *Drymoglossum acrostichoides* (Hook. & Grev.) T. Moore, Index Fil.: 31. 1857. TYPE: South Africa. Cape of Good Hope, *D. Thom s.n.* [Hb. Hook] (holotype, K!). Figure 1A.

Elaphoglossum falcatum (Fée) T. Moore, Index Fil.: 9. 1857. *Acrostichum falcatum* Fée, Mém. Foug., 2: 44, tab. 21(1). 1844 [1845]. TYPE: Bourbon [Réunion]. *Lépervanche-Mézières & Richard s.n.* [Hb. Bory 27,49] (holotype, P!).

Elaphoglossum inversum (Cordem.) H. Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. 36(1): 146. 1899. *Acrostichum inversum* Cordem., Fl. Réunion, part 1: 84. 1891. TYPE: Réunion. Grande Montée de la Plaine des Cafres, 1899, *E. J. de Cordemoy s.n.* pro parte, 2 right-hand specimens only (lectotype, designated here, P!).

Fronds moderately spaced 0.8–1.5 cm distant, borne in 2 ranks; rhizome long-creeping, 2–4 mm diam., occasionally branching, densely paleaceous; scales 3–5 × 1.2–1.6 mm, ovate to ovate-elliptic, brown with dark brown bands at base and apex (or often almost completely dark and only margins clearer), very often lustrous, base truncate, cordate, or auriculate, apex acuminate, margins entire or bearing toward base short teeth or bulbous-tipped cilia, cells small, rectangular. Phyllopodia to 6–10 mm long, slightly swollen, brown to dark brown, paleaceous; sterile fronds 10–25(–41) cm; stipe 3–12 cm, canaliculate, narrowly winged distally, brown to blackish, bearing scattered caducous scales like those of rhizome; blade narrowly elliptic to oblong, often somewhat falcate, 7–16(–26) × 0.7–2(–3) cm, base narrowly cuneate to attenuate, apex acute to long-acuminate, coriaceous to subcoriaceous, costa prominulous, rounded abaxially, canaliculate adaxially, margins revolute, veins distinct to somewhat indistinct, free with thickened tips, adaxial surface of blade glabrate, abaxial surface of blade bearing scattered, brown, ovate scales 3–4 × 2 mm with margins dentate to ciliate mixed with smaller substellate scales with glandular marginal cilia. Fertile frond 9–26(–40) cm long; stipe slender, about half total frond length; blade 6–16(–25) cm, narrowly elliptic, falcate, base narrowly cuneate, decurrent, apex acute. Spores 35–40 × 20–25 μm (excluding perispore), perispore cristate, crests 3–6 μm high, with entire to finely sinuate margins.

Distribution and habitat. Réunion; also known from Madagascar, the Comoro Islands, tropical and southern Africa, Sao Tomé, and Fernando Po. In Réunion *E. acrostichoides* occurs from 1200 to 2300 m in moist and wet forests and ericoid formations as an epiphyte and saxicolous on mossy rocks.

Discussion. Elaphoglossum acrostichoides greatly resembles *E. coursii* by its general appearance, but differs by paler, less stiff rhizome scales. *Elaphoglossum acrostichoides* resembles *E. angulatum* by the long-creeping rhizome, but differs by less widely spaced fronds. *Elaphoglossum acrostichoides* can be distinguished from the other species in the Mascarenes by non-appressed, dark-streaked rhizome and stipe scales. In Réunion it hybridizes with *E. coursii* (Lorence, 1984), forming *E.* ×*cadetii*

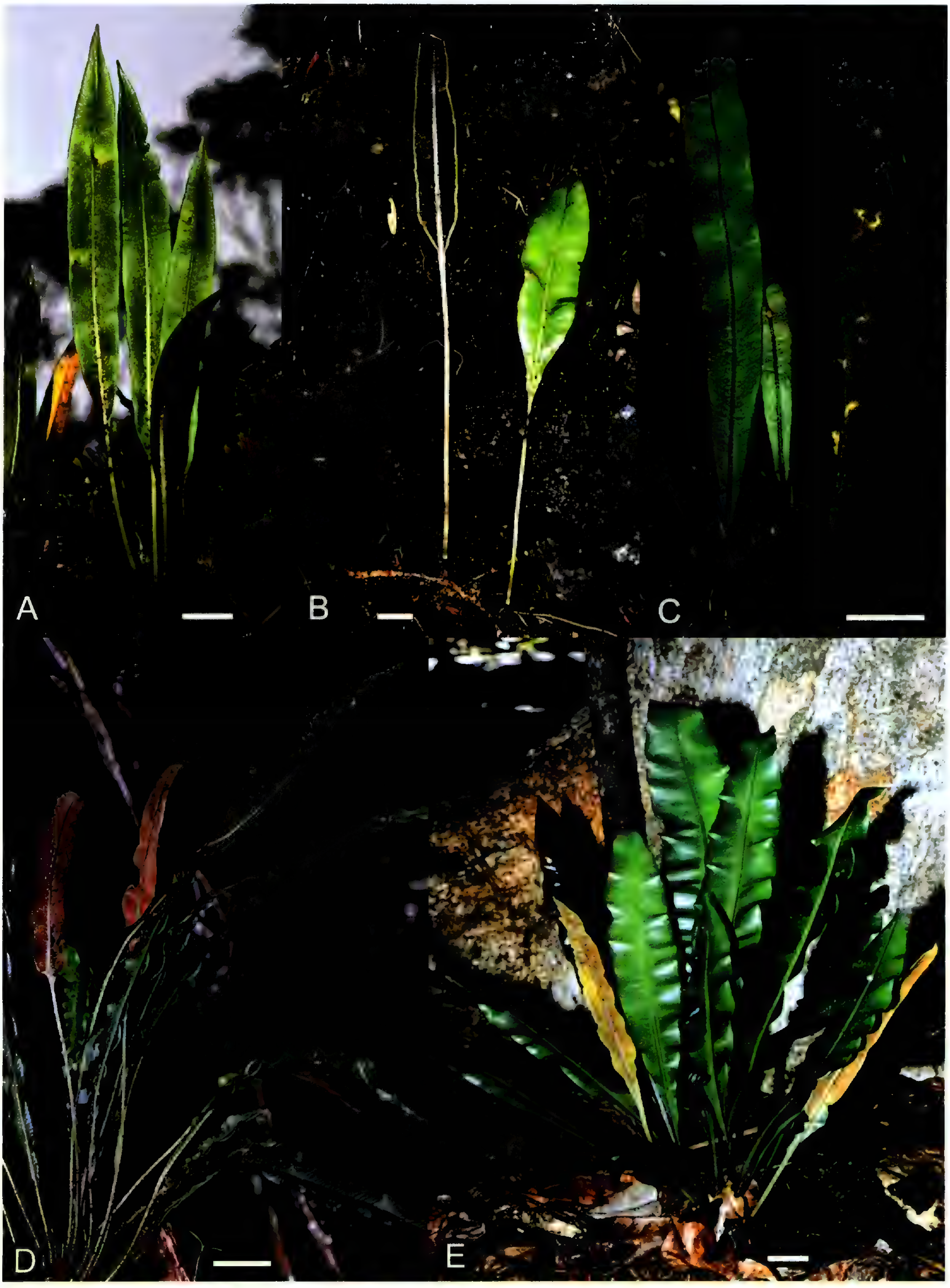


Figure 1. Habit of some Mascarene *Elaphoglossum* species. All the illustrations show specimens with sterile and fertile fronds. —A. *E. acrostichoides* from Réunion, *Rouhan & Grangaud 249.* —B. The long-creeping rhizome of *E. angulatum* from Réunion, *Rouhan 216.* —C. *E. richardii* from Réunion, *Rouhan et al. 231.* —D. *E. aubertii* from Réunion, *Rouhan et al. 241.* —E. *E. sieberi* from Mauritius, Brise Fer Reserve. Scale bars = 2 cm.

Lorence. *Elaphoglossum acrostichoides* resembles *E. glabellum* J. Sm. from the Neotropics in nearly all characters; certain specimens of *E. acrostichoides* are indistinguishable from the Neotropical ones (Moran & Smith, 2001). We found in the Paris herbarium only one sheet bearing the name *Acrostichum inversum* along with the annotations "La Réunion" and "Jacob de Cordemoy," and the date "1899" on the label is subsequent to the original publication (1891). Of the four specimens included on this sheet, the two right-hand specimens only are *Elaphoglossum acrostichoides* (the two left-hand remaining specimens being *E. angulatum* (Blume) T. Moore), necessitating the need to designate a lectotype (ICBN, Art. 9.9; Greuter et al., 2000). We hereby designate these two right-hand specimens of *E. J. de Cordemoy s.n.* as the lectotype of *Acrostichum inversum* Cordem., herein referred to *E. acrostichoides* (Hook. & Grev.) Schelpe.

Selected specimens examined. RÉUNION. Bébour, *Lorence in MAU 15623* (MAU); near Rivière des Marsouins, *Lorence in MAU 15614* (MAU); path to Piton de Bébour, *Lorence in MAU 15621* (MAU); Col de Bébour, *Cadet 4028* (REU); Boucan Launay, *Boivin 801* (P); Cilaos, au dessus des Thermes, *Cadet 4122* (REU); Grand Matarum, *Cadet 805* (P); pente du Cirque, *Cadet 1929A* (P); sentier GR R1 entre "Le Bloc" et le gîte de la Caverne Dufour, *Rouhan 215* (NY, P); Cirque de Salazie, *Rouhan et al. 229* (P, PTBG); Dimitile, *Rouhan & Grangaud 204* (P); Grand Bénard, Pic Maïdo, *Cadet 1749* (P); Grand Matarum, *Lorence in MAU 15637* (MAU); Ilet à Guillaume, *Badré 866* (P); Piton des Neiges, *Lorence in MAU 15648* (MAU, MO); sentier de la rivière, *Rouhan & Grangaud 249* (NY, P, PTBG); Plaine des Fougères, Oct. 1850, *Boivin s.n.* (P); Salazie, *Lépervanche-Mézières s.n.* (P); sentier de la Roche Ecrite, *Badré s.n.* (P); St. Paul, sentier de l'îlet Alcide, *Rouhan et al. 242* (NY, P, PTBG); volcan (Massif de la Fournaise), Pas de Bellecombe, *Lorence & Lorence 2520* (MO).

2. Elaphoglossum ×adulterinum Lorence [*Elaphoglossum lanatum* (Bojer ex Baker) Lorence × *E. tomentosum* (Bory ex Willd.) H. Christ], Fern Gaz. 12: 347, fig. 4. 1984. TYPE: Mauritius. Valley of Cascade 500 Pieds (Cascade Alexandra), 1974, *D. H. Lorence 874* (holotype, MAU 16309!).

Fronds caespitose, spaced 3–5 mm distant, borne in 2 ranks; rhizome short-creeping, 2–3 mm diam., rarely branched, densely paleaceous apically; scales 4–6 × 0.4–0.6 mm, narrowly ovate to lanceolate, castaneous, opaque, base cordate to auriculate, entire or bearing clear, globose marginal glands, apex narrowly acuminate, filiform, sinuate, margins sparsely glandular dentate-ciliate, cells opaque. Phyllopodia 6–8 mm long, thickened, dark brown, paleaceous basally; sterile fronds (27–)35–48.5 cm; stipe (8–)10–15 cm, 0.5–1 mm diam., stramineous, canaliculate, bearing scattered, appressed, brown caducous ovate scales 1–2 × 0.5 mm, base obtuse, apex acute, margins scarious, glandular-ciliate, these intermixed with smaller, matted scales; blade linear-oblong to linear, (19–)25–32 × (1.4–)1.8–2.5 cm, base narrowly cuneate, decurrent, apex acute to acuminate, subcoriaceous, costa stramineous, prominulous and rounded abaxially, shallowly canaliculate adaxially, both surfaces covered with a homogenous layer of thin, matted, appressed pale brown to buff-colored, ovate to subcircular scales 1–1.5 × 1 mm, basifixed, base rounded to cordate or sagittate, base and margins bearing long, spreading arachnoid cilia, pedicel and center darker brown, subtended by cluster of globose glands, cells hyaline, thin-walled, adaxial surface of lamina glabrescent, veins unbranched or bifurcate, in part free apically with tips thickened, in part uniting submarginally, both surfaces of blade with scattered hair-toothed to deltoid scales 0.2–0.5 mm long, glandular-ciliate at base. Fertile frond 20–25 cm long; stipe 10–11.5 cm, 1 mm diam.; blade 11–14 × 0.7–1 cm, linear-elliptic, chartaceous, base narrowly cuneate, apex acute, adaxial surface with dense layer of matted scales as in sterile frond, margins revolute. Spores 82% aborted, normal spores 35–38 × 25–27 μm (excluding perispore), perispore cristate, crests low, 1.5–3 mm high, sinuate to finely erose-dentate.

Distribution and habitat. Elaphoglossum ×adulterinum is known only from the type locality in Mauritius at the southern extremity of the central plateau, altitude 600 m. The hybrid occurs on boulders below cliffs in wet forests where the parental species *E. lanatum* and *E. tomentosum* occur nearby (Lorence, 1984).

Discussion. Elaphoglossum ×adulterinum resembles *E. tomentosum* in its habitat preference (epiphytic or epipetric), erect fronds, and sterile blade shape, although its rhizome scales are glandular and resiniferous as in *E. lanatum*. The hybrid's mixed venation, in part free as in *E. lanatum* and in part uniting intramarginally as in *E. tomentosum*, and intermediate frond scale morphology distinguish it from the parents.

Specimens examined. MAURITIUS. Valley of Cascade 500 Pieds (Cascade Alexandra), *Lorence sub MAU 16307* (MAU, MO), *Lorence 1609* (MO), *Lorence 1610* (MO), *Lorence 847* (MAU).

3. Elaphoglossum angulatum (Blume) T. Moore, Index Fil.: 5. 1857. *Acrostichum angulatum* Blume, Enum. Pl. Javae 101. 1828; Fl. Javae

3: 25 (1828), tab. 6 exhibiting a drawing of the type specimen. *Olfersia angulata* (Blume) C. Presl, Tent. Pterid. 234. 1836. TYPE: Java. *C. L. von Blume s.n.* (holotype, K!). Figure 1B.

Elaphoglossum alstonii Tardieu, Notul. Syst. 15: 433. 1959. *Acrostichum laurifolium* Fée, Mém. Foug., 2: 36, tab. 7. 1844 [1845], non *Acrostichum laurifolium* Thouars, Esquisse Fl. Tristan d'Acugna: 31. 1803. TYPE: Bourbon [Réunion]. 1840, *Lépervanche-Mézières 14* [Hb. Bory 27,15] (holotype, P!).

Elaphoglossum inversum (Cordem.) H. Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. 36(1): 146. 1899. *Acrostichum inversum* Cordem., Fl. Réunion, part 1: 84. 1891. TYPE: Réunion. Grande montée de la Plaine des Cafres, 1899, *E. J. de Cordemoy s.n.* pro parte, 2 left-hand specimens only (lectotype, designated here, P!).

Fronds widely spaced 1.5–4 cm distant, erect, borne in 2 ranks; rhizome always very long-creeping, 2–3 mm diam., occasionally branching, clothed with appressed scales; scales 3–5 × 2–3 mm, ovate, thin, light brown or reddish brown, base auriculate with overlapping lobes, apex acute to acuminate, margins entire or bearing toward base rare, short bulbous-tipped cilia, cells squarish. Phyllopodia to 15 mm long, slightly swollen, brown to dark brown, paleaceous; sterile fronds 20–40 cm; stipe 9–17 cm, canaliculate, brown to orange, bearing scattered spreading, light brown, ovate scales; blade narrowly elliptic to narrowly ovate, 10–16 × 2–4 cm, base narrowly cuneate, shortly decurrent, apex acute to acuminate, coriaceous to subcoriaceous, costa prominulous, rounded to angled abaxially, canaliculate adaxially, margins revolute, veins often indistinct, in part free apically with thickened tips and in part uniting into an intramarginal commissure, adaxial surface of blade glabrate, abaxial surface of blade bearing a few scattered, ovate scales 1–3 mm long. Fertile frond 20–40 cm long; stipe as in sterile, blade as in sterile but narrower. Spores 28–30 × 20–23 μm (excluding perispore), perispore cristate, crests 4–5 μm high, with entire to finely sinuate margins.

Distribution and habitat. Réunion: also Madagascar, tropical Africa, southern India, Sri Lanka, Java, Sumatra, Borneo, New Guinea, Philippines, New Caledonia, and Taiwan. In Réunion, *Elaphoglossum angulatum* occurs as an epiphyte or casually terrestrial in ericoid formations from 1300 to 2200 m.

Discussion. This species resembles *Elaphoglossum acrostichoides* by the long-creeping rhizome and general appearance, but differs by more widely spaced fronds. *E. angulatum* can also be distinguished by its ovate, appressed, uniformly colored, light brown or reddish brown rhizome and stipe scales, by the veins in part uniting into an intramarginal commissure, and by the erect fronds (see Sledge, 1967, for more details).

The type of *Acrostichum angulatum* is from Java and was collected by Blume. Carl Ludwig von Blume worked at Leiden (L), and according to Stafleu and Cowan (1976) all his collections were deposited in L. Nevertheless, many specimens were distributed from Leiden after his death, and not always with the regard we now have for type specimens (P. Hovenkamp (L), pers. comm.). There is a specimen of *Blume s.n.* housed in K and bearing a label "Herb. Lugd. Batav." with the mention "Acrost. angulatum" written by Blume. Furthermore, this specimen matches well the drawing of the type specimen in *Flora Javae.* For these reasons, this specimen of *Blume s.n.* housed in K is identified as the holotype of *Acrostichum angulatum* Blume.

Concerning the typification of *Acrostichum inversum*, although the date "1899" written on the label is posterior to the original publication (1891), we found in the Paris herbarium only one sheet bearing the name *Acrostichum inversum* along with the annotations "La Réunion" and "Jacob de Cordemoy." Of the four specimens included on this sheet, the two left-hand specimens only are *Elaphoglossum angulatum* (the two right-hand remaining specimens are *E. acrostichoides*), necessitating the need to designate a lectotype (ICBN, Art. 9.9; Greuter et al., 2000). We hereby designate these two left-hand specimens of *E. J. de Cordemoy s.n.* as the lectotype of *Acrostichum inversum* Cordem., here referred to *E. angulatum* (Blume) T. Moore.

Selected specimens examined. RÉUNION. Bébour, near Rivière des Marsouins, *Lorence in MAU 15640* (MAU, MO); Cilaos, sentier GR R1 entre "Le Bloc" et le gîte de la Caverne Dufour, *Rouhan 216* (NY, P, PTBG); pente du Cirque, *Cadet 1930* (P); Plaine des Palmistes rd., *P. O. Wiehe 1721* (MAU); Piton des Neiges, *Lorence in MAU 15612* (MAU), *Lorence in MAU 15615* (MAU), *Lorence 408* (MO); Plaine des Cafres, près de la source Reillac, *Cadet 1778* (P); Plaine des Fougères, *Rouhan et al. 233* (P); Plaine des Palmistes, la Grande Montée, *Cadet 504* (P); volcan, Enclos Fouqué, *Cadet 1556* (P, top 3 specimens); volcan, Pas de Bellecombe, *Rouhan & Grangaud 220* (NY, P).

4. Elaphoglossum aubertii (Desv.) T. Moore, Index Fil.: 5. 1857. *Acrostichum aubertii* Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5: 309. 1811. TYPE: Bourbon [Réunion]. 1808, *A. Du Petit-Thouars s.n.* (holotype, P-JU 992!). Figure 1D.

Fronds caespitose, borne in 3 ranks; rhizome very short-creeping, 2–3 mm diam., rarely branched, densely paleaceous; scales 6–8 × 0.5–

1 mm, narrowly ovate to oblong, dark reddish brown, base cordate, apex narrowly acuminate, margins entire, cells fusiform, to very linear for the marginal cells. Phyllopodia 2–3 mm long, slightly flattened and constricted, dark brown to black; sterile fronds 10–30 cm; stipe 2–6 cm, 0.5–1 mm diam., stramineous, canaliculate, bearing scattered to abundant, reddish brown, narrow, spreading subulate scales 3–5 mm long, 0.25–0.5 mm wide, base tubular and closed, apex long-acuminate, margins with short, glandular-tipped cilia basally, entire above; blade linear-oblong, 8–24 × 0.8–1.4 cm, base cuneate to narrowly cuneate, apex acute to rounded, chartaceous, costa prominulous and rounded abaxially, shallowly canaliculate adaxially, both surfaces bearing spreading subulate scales as in stipe, margins thin, flat, translucent, bearing fringe of reddish brown, spreading scales as on costa, veins distinct, unbranched or bifurcate, free apically, tips thickened and dark, both surfaces of blade with scattered subulate to deltoid scales 0.2–0.5 mm long, glandular-ciliate at base. Fertile frond about equaling or slightly shorter than sterile frond; stipe slender, 2 to 3 times longer than sterile stipe; blade 3–7 × 0.7–1.4 cm, narrowly ovate to narrowly elliptic, base cuneate to truncate or rarely subcordate, apex acute, costa sparsely and minutely paleaceous on both surfaces, sporangia lacking on margins and extreme base of blade. Spores 34–38 × 22–25 μm (excluding perispore), perispore surface echinate, spinules 2.5–4 μm high.

Distribution and habitat. Réunion; also known from Madagascar, Comoro Islands, tropical and southern Africa, Fernando Po, and São Tomé. On Réunion this species occurs in wet forests and ericoid shrubland from 200 to 1500 m elevation. The occurrence of *E. aubertii* on Mauritius is doubtful and based on a single specimen (*Boivin s.n.*), the type of *A. boivinii* Mett. ex Kuhn (Filic. Afr. 43. 1868), which has not been located. No other collections are known from Mauritius.

Discussion. *Elaphoglossum aubertii* can be distinguished by spreading, subulate scales, conspicuous hydathodes, and short petioles (⅛ to ¼ the length of the blades).

Elaphoglossum aubertii greatly resembles *E. eximium* (Mett.) H. Christ, a species of South and Central America (Moran & Smith, 2001). Both species show morphological characters so similar that distinction is very difficult without knowing the geographical origin. This close relationship is strongly supported by phylogenetic analyses based on molecular data, since *E. aubertii* and *E. eximium* appear more closely related to each other than to any other species in the genus (Rouhan et al., 2004). Thus, *E. aubertii* may possibly be conspecific with *E. eximium* (in which case *E. aubertii* would have priority).

Selected specimens examined. RÉUNION. Bébour, *Lorence in MAU 15629* (MAU); Plateau de Bébour, *Bosser 21503* (P); Dimitile, *Rouhan & Grangaud 206* (P); Forêt du Tévelave, *Cadet 123* (P); Montée de la Plaine des Cafres, *Bosser 9544* (P); Piton, Mare à Boue, Plaine des Cafres, *Bosser 21759* (P); Plaine des Fougères, *Rouhan et al. 226* (NY, P, PTBG); Saint-Philippe, Basse Vallée, *Badré 1004* (P); St. Paul, sentier de l'îlet Alcide, *Rouhan et al. 241* (NY, P).

5. Elaphoglossum ×cadetii Lorence [*Elaphoglossum acrostichoides* (Hook. & Grev.) Schelpe × *E. coursii* Tardieu], Fern Gaz. 12: 346, fig. 3. 1984. TYPE: Réunion. Piton de la Fournaise, Plaine des Sables, *T. Cadet 2063* (holotype, REU!; isotype, P not seen).

Fronds spaced 2–4 mm distant, borne in 2 ranks; rhizome short-creeping, 2–4 mm diam., rarely branching, densely paleaceous; scales 2–4 × 0.5–1 mm, ovate, shiny black, base cordate or auriculate, pale brown, apex acute to acuminate, black and opaque, margins bearing rare glandular-tipped cilia. Phyllopodia to 5–7.5 mm long, swollen, dark brown to black, paleaceous toward base; sterile fronds (6–)8–14 cm; stipe (2.2–)3.6–6.5 cm × 0.5–1 mm, canaliculate, stramineous, bearing scattered dark brown, discolorous ovate scales 2–3 × 0.5–1 mm, margins sparsely ciliate; blade narrowly elliptic, 4–10 × 0.7–1.5 cm, base narrowly cuneate, narrowly decurrent, apex acute with rounded tip, coriaceous, costa prominulous, rounded abaxially, slightly canaliculate adaxially, margins revolute, veins indistinct, dichotomous, apically free with thickened tips, adaxial surface of blade glabrate, abaxial surface bearing minute brown, substellate scales 0.5 mm diam., with a few larger scales along costa. Fertile frond 14–18.5 cm long; stipe 7.5–14 cm, about three times longer than sterile stipe; blade 6–8.5 × 0.9–1 cm, narrowly elliptic, base narrowly cuneate, slightly decurrent, apex obtuse, costa stramineous, veins indistinct. Spores ca. 90% aborted.

Distribution and habitat. Réunion, known only from the type collection. *Elaphoglossum ×cadetii* represents a natural hybrid between *E. acrostichoides* and *E. coursii,* which both occur at the type locality on the Piton de la Fournaise massif, an active volcano (Lorence, 1984). The putative hybrid was collected from fissures in lava at 2300 m among heath vegetation. A morphologically similar collection from Mt. Ankaroka, Madagascar (*H. Humbert & G. Cours*

17521, P!), may represent this hybrid, as both putative parents also occur in Madagascar.

Elaphoglossum ×*cadetii* resembles *E. coursii* but differs by its longer, narrower rhizome scales, shorter coriaceous sterile fronds with indistinct veins, and fertile fronds up to twice as long as the sterile ones.

6. Elaphoglossum coursii Tardieu, Notul. Syst. 15: 434. 1959. TYPE: Madagascar. 1951, *H. Humbert & R. Capuron 24918* (holotype, P!; isotype, K!).

Fronds moderately spaced 0.5–1 cm distant, borne in 2 ranks; rhizome moderately long-creeping, 1–3 mm diam., occasionally branching, sparsely paleaceous; scales 1–1.5 × 0.4–0.7 mm, ovate to ovate-elliptic, dark brown to black, paler at base and margins, opaque, rigid, base auriculate with overlapping lobes, apex acute, margins with bulbous-tipped cilia especially basally, cells square to fusiform. Phyllopodia 5–10 mm long, slightly swollen, brown to blackish, paleaceous; sterile fronds 20–35 cm; stipe 6–15 cm, slender, canaliculate, stramineous to dark brown, bearing scales like those of rhizome but larger and paler; blade linear-elliptic to linear, 10–24 × 0.6–1.8 cm, base narrowly acute, attenuate and decurrent, apex acute to long-acuminate, subcoriaceous to coriaceous, costa prominulous and rounded to angulate abaxially, canaliculate adaxially, margins strongly revolute, veins distinct to somewhat indistinct, often bifurcate, apically free, adaxial surface of blade glabrous, abaxial surface of blade bearing scattered, small brown, substellate scales 0.2–1 mm diam. with glandular marginal cilia. Fertile frond 20–35 cm long, equaling or slightly shorter than sterile frond; stipe slender, slightly longer than sterile stipe; blade linear-elliptic to linear-obovate, base narrowly cuneate, decurrent, apex acute, mucronulate. Spores 40–45 × 30–35 μm (excluding perispore), perispore cristate, crests 4–8 μm high, rounded, margins entire to finely sinuate.

Distribution and habitat. Réunion; also known from Madagascar, Comoro Islands, and Zambia. On Réunion *E. coursii* is known from 400 to 2000 m and is epiphtyic or saxicolous in open wet forests and ericoid formations.

Discussion. Elaphoglossum coursii greatly resembles *E. acrostichoides*, but it can be distinguished by its darker, lustrous, and stiffer rhizome scales.

Specimens examined. RÉUNION. Cilaos, au dessus des Thermes, *Cadet 4126* (REU); Dimitile, SE rim of Cirque de Cilaos caldera, N of Entre-Deux & Ravine des Citrons, *Lorence et al. 7561* (MAU, PTBG); Grande Jument, sentier, *Rouhan & Grangaud 199* (P); Haut de Saint Benoit, cratère, *Bosser 21012* (P).

7. Elaphoglossum heterolepis (Fée) T. Moore, Index Fil.: 10. 1857. *Acrostichum heterolepis* Fée, Mém. Foug., 2: 56, tab. 15(1). 1844 [1845], non *Acrostichum heterolepis* Baker, Syn. Fil. 521. 1874. TYPE: Mauritius. *Sieber Flora Mixta 281* (lectotype, designated by Rouhan & Lorence (2003: 838), PR!). Figure 2A, C.

Fronds caespitose, spaced 4–10 mm, borne in 2 ranks; rhizome short-creeping, 4–5 mm diam., profusely branched, densely paleaceous; scales 6–12 × 0.5–0.7 mm, narrowly ovate, shiny dark brown to black with clear or white borders, spreading, persistent, base cordate to auriculate, apex slender, acute, margins entire, central cells fusiform, opaque (Fig. 5A). Phyllopodia 3–6 cm long, chocolate to blackish brown, bearing at base scales as in rhizome; sterile fronds 22–40(–55) cm; stipe 7–14(–16) cm, 1.5–2.5 mm diam., reddish to orange-brown, canaliculate, winged in distal half, densely paleaceous with reddish brown to black, narrowly ovate, often falcate scales 3–6 × 0.5–1 mm, base truncate to auriculate and bearing a few hair teeth, apex long-acuminate, margins entire, scarious, whitish to yellowish; blade linear-ovate to linear-elliptic or linear-obovate, 20–40(–50) × 2.6–3.6(–4) cm, base narrowly cuneate, attenuate, apex long-acuminate to caudate, chartaceous, costa prominulous and rounded abaxially, prominulous and shallowly canaliculate adaxially, bearing basally scales as in stipe, margins rounded, slightly revolute, veins unbranched or bifurcate, apically free, tips thickened, both surfaces of young blade covered by a thin continuous layer of appressed, beige to gray scales of two types, the small ones 0.5 mm diam., ovate to orbicular, peltate, scarious, sometimes with brown centers, margins densely ciliate-fimbriate with hair teeth (Fig. 5C), the larger scales often concentrated along the costa, 1.5–3 × 0.5 mm, narrowly ovate, sometimes with brown centers, base flabelliform, margins densely fimbriate-ciliate, the cells thin-walled, translucent (Fig. 5B), adaxial blade surface glabrescent. Fertile frond 34–50(–62) cm long; stipe 1.5 times longer than sterile stipe; blade 14–25(–28) × 1.4–2.5(–2.8) cm, linear-elliptic, base narrowly cuneate to attenuate, apex acute to obtuse, adaxial surface blade and abaxial surface stipe bearing dense layer of rusty-colored scales as in sterile frond, intersporangial scales very often present. Spores 43–45 × 23–30 μm (excluding perispore), perispore cristate, 5–10

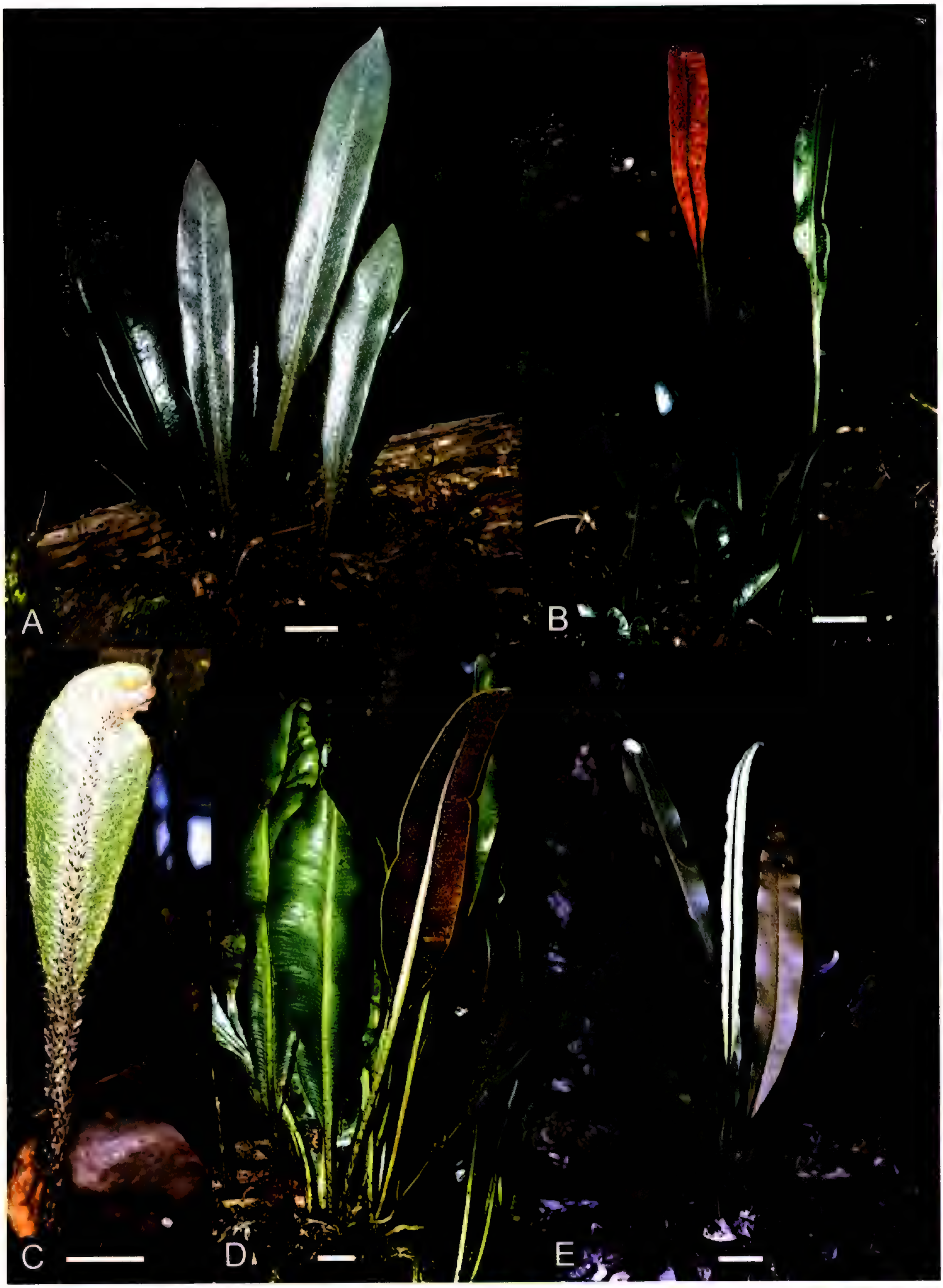


Figure 2. Habit of some Mascarene *Elaphoglossum* species. Except for *E. heterolepis*, all the illustrations show specimens with sterile and fertile fronds. —A, C. *E. heterolepis* with its bi-colored stipe scales and both surfaces of young blade covered by a thin continuous layer of appressed, beige to gray scales, from Mauritius, same population as *Rouhan 177*. —B. Typical longer fertile fronds of *E. lepervanchei* from Mauritius, same population of *Rouhan et al. 175*. —D. *E. macropodium* from Réunion, same population as *Rouhan et al. 232*. —E. *E. tomentosum* from Mauritius, same population as *Rouhan et al. 180*. Scale bars = 2 cm.

μm high with finely crisped margins and spinulose surface.

Distribution and habitat. Réunion and Mauritius. Epiphytic to 10 m above ground or occasionally terrestrial, often forming dense clumps, rarely saxicolous. Common on both islands from 200 to 1400 m elevation in moist and wet forests.

Discussion. This species resembles *Elaphoglossum tomentosum* by the blade covered by a thin continuous layer of appressed scales. Nevertheless, *E. heterolepis* differs clearly from all other Mascarenes species by its apically free veins, two types of frond scales, and slender, elongated bicolorous rhizome scales with dark centers and whitish borders. On Mauritius it hybridizes with *E. tomentosum* (Lorence, 1984).

Since *Elaphoglossum heterolepis* is similar to *E. tomentosum*, Baker did not distinguish both species in his book *Synopsis Filicum* (1874). Therefore, in his treatment the name *Acrostichum heterolepis* Fée appears as a synonym of the earlier published name *A. tomentosum*. Consequently, *A. tomentosum* was misapplied and used in place of the correct name *E. heterolepis* in the following treatments: *Acrostichum tomentosum* sensu Bojer, Hortus Maurit. 413. 1837; sensu Cordem., Fl. Réunion, part 1: 85. 1891, Fl. Réunion. 96. 1895, non *Acrostichum tomentosum* Bory ex Willd. *Elaphoglossum heterolepis* is also the correct name for plants misidentified by Tardieu as *E. obductum* (Kaulf.) T. Moore and figured in her treatment in Notul. Syst. 15(4): 429, tab. 3(6–11). 1959. Typification of the name *E. heterolepis* is discussed in greater detail by Rouhan and Lorence (2003).

Selected specimens examined. MAURITIUS. Alexandra Falls, *Rouhan et al. 177* (MAU, NY, P); Bel Ombre, *Lorence 1402* (MO); Kanaka Crater, *Lorence 1078* (MO); Macabé forest, *Lorence 1420 in MAU 17544* (K, MAU, MO); Macabé-Brise Fer rd., *Lorence in MAU 16019* (K, MAU, P); Macabé, sentier menant à la Mare aux Joncs, *Rouhan et al. 179* (MAU, NY, P, PTBG); Mare Longue Plateau, *Lorence 2.11* (MO); Mt. Lagrave, E flank, *Lorence 783 in MAU 16317* (K, MAU); flank facing Eau Bleu reservoir, *Lorence in MAU 18785* (MAU); Pétrin Nat. Reserve, rd. to Grand Bassin, *Lorence in MAU 15816* (MAU, MO, REU); Piton Grand Bassin, *Lorence in MAU 14599* (MAU); Piton Grand Fond, *Lorence 300* (MO); Plaine Champagne, rd. to Bel Ombre, *Lorence in MAU 16018* (MAU); Bassin Blanc, path from Les Mares, *Lorence in MAU 14609* (MAU). RÉUNION. Basse Vallée (St. Philippe), *Cadet 3790* (P, REU); Bébour, path to Piton Bébour, *Lorence in MAU 15645* (MAU); Boucan Launay, *Boivin 800* (P); Brûlé de Sainte Rose, *Badré 985* (P [2]); Brûlé, *Bédier 53* (P); Chemin Arnoux, *Cadet 880* (P); Cilaos, *Cadet 1930bis* (P); Dimitile, *Rouhan & Grangaud 202* (P); Mare Longue–St. Philippe, *Schlieben 10934* (MAU); Morne des Patates Durand, *Lorence in MAU 15619* (MAU); Plaine des Fougères, 1850, *Boivin s.n.* (P); Route du Grand Etang, *Badré 896* (P); Salazie, 1886, *Keller s.n.* (P); Takamaka, *Cadet 1702* (P); Tremblet, *Rouhan & Grangaud 211* (NY, P).

8. Elaphoglossum ×heterophlebium Lorence [*Elaphoglossum heterolepis* (Fée) T. Moore × *E. tomentosum* (Bory ex Willd.) H. Christ], Fern Gaz. 12: 343, fig. 2. 1984. TYPE: Mauritius. Pétrin Nat. Reserve, 1973, *D. H. Lorence 14.2 in MAU 15821* (holotype, MAU!).

Fronds caespitose, borne in 2 ranks; rhizome short-creeping, 5 mm diam., occasionally branched, densely paleaceous; scales 5–7 × 0.5–0.7 mm, narrowly ovate to lanceolate, slightly falcate, castaneous, thick, base cordate, apex long-acute, filiform, margins scarious, bearing sparse short hair teeth or rare glandular cilia, cells opaque. Phyllopodia 1–2 cm long, dull brown, paleaceous as in rhizome; sterile fronds 33–45 cm; stipe 8–13 cm, 1.5–2 mm diam., stramineous, adaxially flattened, densely paleaceous when young, scales narrowly ovate, falcate, 2–5 × 0.8–1.5 mm, base peltate and obtuse, or basifixed and cordate or auriculate, apex acute, centers dark castaneous, opaque, margins scarious pale brown, fimbriate to ciliate-dentate with hair or glandular-tipped teeth; blade oblong-elliptic or lanceolate, 22.5–32 × 2.6–3.4 cm, base narrowly cuneate, apex acute to slightly acuminate, subcoriaceous, costa prominulous on both surfaces, rounded abaxially, slightly canaliculate adaxially, margins rounded, slightly revolute, veins bifurcate, in part free with thickened tips, in part anastomosing into intramarginal arcs, both surfaces of blade covered by a thin, persistent homogeneous layer of closely appressed, matted, ovate to subcircular, peltate scales 0.5–1 × 0.5 mm, buff-colored, hyaline, base and margins fimbriate with arachnoid cilia 0.1–0.3 mm long with acicular or bulbous tips, cells thin-walled. Fertile frond 32.5–36 cm long; stipe 16.5–19.5 cm long; blade 16–16.5 × 1–1.5 cm, linear-elliptic, base and apex acute, adaxial blade surface bearing thin layer of scales as in sterile frond. Normal spores 35–38 × 25–27 μm (excluding perispore), perispore cristate, 2–3 μm high with minutely spinulose margins; 52%–85% of spores aborted.

Distribution and habitat. Mauritius, known from four scattered localities on the central plateau at 600 to 700 m in wet forests and *Philippia* Klotzsch heath formations. In all cases, the nothospecies was growing terrestrially close to one or both parental species, *E. heterolepis* and *E. tomentosum*.

Discussion. Specimens of *Elaphoglossum ×heterophlebium* are remarkably uniform morphologi-

cally. Although tending to resemble *E. heterolepis* somewhat more than *E. tomentosum*, *E.* ×*heterophlebium* is intermediate between both parents regarding color and shape of the scales and the veins, which are in part free with thickened tips (resembling *E. heterolepis*) and in part uniting into intramarginal arcs (resembling *E. tomentosum*).

Specimens examined. MAURITIUS. Brise Fer rd., *Lorence 16.2 in MAU 15819* (MAU); Plaine Champagne, *Lorence sub MAU 15099* (MAU), *Lorence 996 sub MAU 16518* (MAU), *Lorence 1544* (MAU, MO); Pétrin Nat. Reserve, *Lorence 14.2 in MAU 15821* (MAU).

9. Elaphoglossum hybridum (Bory) Brack., U.S. Expl. Exped., Filic. 16: 69. 1854. *Acrostichum hybridum* Bory, Voy. Iles Afrique. 3: 95. 1804, non *Elaphoglossum hybridum* (Bory) T. Moore, Index Fil.: 10. 1857. *Olfersia hybrida* (Bory) C. Presl, Tent. Pterid. 235. 1836. TYPE: Bourbon [Réunion]. Caverne le Gentil, *Bory de St. Vincent s.n.* [Hb. Bory 27,7] (holotype, P!). Figure 4A.

Although the specific epithet *hybridum* means "of hybrid origin," its application to this taxon is not clear. The author of the basionym, Bory, does not explain why he chose this specific epithet. Furthermore, no evidence supports a hybrid origin for this species, as the morphology is not intermediate between other species in the region, and the spores are not aborted. The names *E. hybridum* var. *cuneatum* Bonap., *E. hybridum* var. *melanopus* Farw., and *E. hybridum* var. *nitidum* (Liebm.) H. Christ have been applied to plants outside the Mascarene area and are not considered herein.

9a. Elaphoglossum hybridum (Bory) Brack. var. **hybridum**

Acrostichum ciliatum Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5: 310. 1811, non *Acrostichum ciliatum* C. Presl, Reliq. Haenk. 1: 15. 1825. TYPE: Bourbon [Réunion]. *P. Commerson s.n.* (lectotype, designated by E. Schelpe (1969: 32), P-JU 1000A!).

Elaphoglossum tricholepis (Baker) C. Chr., Index. Filic.: 317. 1905. *Acrostichum tricholepis* Baker, J. Bot. 1891: 5. 1891. TYPE: Madagascar. Bekilus Mtns., *J. T. Last s.n.* (holotype, K!).

Fronds densely caespitose, borne in 4 ranks; rhizome very short-creeping, 10–12 mm diam., unbranched, densely paleaceous; scales 5–10 × 1–3 mm, narrowly to oblong-ovate, brown, scarious, base truncate to cordate, apex long-acuminate, margins entire or with a few short teeth, base with several short bulbous-tipped cilia, cells squarish to linear-oblong. Phyllopodia 8–18 mm long, swollen basally, black; sterile fronds 25–30(–55) cm; stipe 7–12(–20) cm, 1–2 mm diam., stramineous to pale brown, slightly canaliculate, bearing a dense layer of squarrose, persistent, subulate, dark brown scales 2–5 × 0.3–0.5 mm, base cochleariform and closed, apex long-acuminate, filiform, margins involute, entire, stipe also with simple capitate and irregularly branched hairs; blade ovate to narrowly ovate, elliptic, or sometimes obovate-oblong, 15–20(–40) × 3.5–4.5(–6) cm, base narrowly to broadly cuneate or sometimes rounded, apex acute to acuminate, chartaceous to coriaceous, costa prominulous and rounded abaxially and bearing scattered subulate scales as in stipe, shallowly canaliculate and glabrous adaxially, margins revolute, bearing fringe of dark brown, spreading, persistent, subulate scales as in stipe, veins prominulous, unbranched or 1 to 2 times dichotomous, apically free, tips thickened, both surfaces of blade bearing short, numerous, simple capitate and branched hairs, adaxially glabrescent. Fertile frond shorter than or nearly equaling sterile frond, 16–26(–33) cm long; stipe slender, about equaling sterile stipe; blade 7–12 × 1.5–2.5 cm, narrowly ovate to narrowly elliptic, base acute to narrowly cuneate, apex acute, adaxial surface with short capitate hairs. Spores 36–38 × 23–25 μm (excluding perispore), perispore cristate, crests 3–7 μm high, margins sinuate, somewhat erose.

Distribution and habitat. Mauritius (400–900 m) and Réunion (600–2200 m); also Madagascar, Comoro Islands, tropical and southern continental Africa, Fernando Po, Tristan d'Acunha, and Gough Island. In the Mascarenes usually found growing on mossy rocks and boulders, rarely terrestrially, in shade of montane wet and cloud forests.

Discussion. Elaphoglossum hybridum var. *hybridum* can be distinguished by blades 3.5–4.5 cm wide, absence of hydathodes, and blades with both surfaces and margins bearing dark brown, spreading, subulate scales.

Elaphoglossum hybridum var. *hybridum* greatly resembles *E. erinaceum* (Fée) T. Moore from the Neotropics (Moran & Smith, 2001). Phylogenetic analyses based on molecular data are inconclusive concerning the relationship between both species (Rouhan et al., 2004). Although both species show morphological characters so similar that distinction is very difficult without knowing the geographical origin, evidence is inconclusive if *E. hybridum* may really be conspecific with *E. erinaceum* (in which case, *E. hybridum* would have priority).

Selected specimens examined. MAURITIUS. Bassin Blanc crater, *Julien in MAU 16494* (MAU); Corps de Gar-

de Mtn., *Guého in MAU 11498* (MAU); Mont Deux Mamelles, *Lorence in MAU 15024* (K, MAU, P, REU); Plaine Champagne–Chamarel rd., headwaters of Rivière Saint Denis, *Julien in MAU 14595* (MAU); Rivier du Poste near Kanaka, *Staub in MAU 11348* (MAU); Ruisseau Commérage, *Rouhan et al. 195* (P); Tamarind Falls reservoir, *Lorence in MAU 15823a* (MAU); valley of Cascade 500 Pieds, *Lorence 1608* (MO). RÉUNION. Bébour, Rivière des Marsouins, *Lorence in MAU 15625A–D* (MAU); sentier de la Rivière, *Rouhan & Grangaud 250* (P); Cilaos, sentier GR R1 entre "Le Bloc" et le gîte de la Caverne Dufour, *Rouhan 217* (NY, P, PTBG); sentier allant à la cascade de Bras Rouge, *Rouhan 239* (P); Dimitile, sentier de la Grande Jument, *Rouhan & Grangaud 198* (P); Grand Matarum, *Lorence in MAU 15626* (MAU); Morne des Patates Durand, *Lorence in MAU 15622* (MAU); Piton des Neiges path, *Lorence in MAU 15635* (MAU); Plaine des Fougères, *Rouhan et al. 228* (NY, P); Saint-Philippe, Basse Vallée, *Badré 1005* (P); Takamaka, trail to Ilet à Bananes, *Lorence & Rolland 6944* (PTBG); volcan, Enclos Fouqué, *Cadet 1556* (isolated fertile frond, P); Crête du Volcan, *Bosser 11857* (P).

9b. Elaphoglossum hybridum var. **vulcani** (Lepervanche ex Fée) H. Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. 36(1): 104. 1899. *Acrostichum hybridum* var. *vulcani* Lepervanche ex Fée, Mém. Foug., 2: 41, tab. 9(3). 1844 [1845]. TYPE: Bourbon [Réunion]. Plaine des Palmistes, Plaine des Cafres, Jun. 1831, *P. Lépervanche-Mézières s.n.* [Hb. Bory 27,7] (holotype, P!).

Sterile fronds 8–12(–21) cm long; stipe 3–6(–13) cm long, 0.5 mm diam., somewhat flexuose, densely paleaceous with small scales 2–3.5 × 0.5 mm with large cells, short brown, capitate hairs also present; blade ovate to ovate-elliptic, 4–6(–11) × 1–2.5(–3.6) cm, surfaces scattered with abundant, short, pale brown, capitate, simple or branched hairs, margins fringed with squarrose subulate scales 1.5–2 mm long. Fertile frond 4 × 1.3–1.5 cm, blade with sporangia often absent from margins and extreme base of blade.

Distribution and habitat. Réunion; also Madagascar and the Comoro Islands. This diminutive variety is restricted to higher elevations (1300–2300 m) than variety *hybridum*. It is usually found growing on shady, mossy rock faces and in grottos.

Discussion. Plants of variety *vulcani* differ from those of variety *hybridum* in their smaller habit and fronds, in the smaller scales, and in the fertile frond with sporangia often absent from margins and the extreme base of the blade. *Elaphoglossum hybridum* var. *vulcani* may, however, represent a depauperate ecotype, since collections intermediate between variety *hybridum* and variety *vulcani* occur on Réunion (e.g., see under var. *hybridum*: Bébour, Rivière des Marsouins, *Lorence in MAU 15625A–D*, MAU).

Selected specimens examined. RÉUNION. Cilaos, sentier GR R1, entre "Le Bloc" et le gîte de la Caverne Dufour, *Rouhan 214* (NY, P); Cratère Commerson, *Rouhan & Grangaud 219* (P, PTBG); Pas de Bellecombe, *Rouhan 222* (NY, P); Pas des Sables, Sep. 1892, *Cordemoy s.n.* (P); path to Piton des Neiges, near le gîte, *Lorence in MAU 15635* (MO); Plateau Kerveguen, *Badré 960* (P); Route forestière de Tévelave, ligne Domaniale, *Lorence 2496* (MAU); Sommet du Grand Bénard, 16 Feb. 1847, *Boivin s.n.* (P).

10. Elaphoglossum lanatum (Bojer ex Baker) Lorence, Fern Gaz. 11: 199, fig. 1a–g. 1976. *Acrostichum viscosum* Sw. var. *lanatum* Bojer ex Baker, Fl. Mauritius: 512. 1877. TYPE: Maurice [Mauritius]. Bois Chéri, *W. Bojer s.n.* pro parte, 4 left-hand specimens only (holotype, K! [Hb. Hook.]). Figure 3B.

Fronds spaced 3–5 mm, borne in 2 ranks; rhizome short-creeping, 2–3 mm diam., rarely branched, resinous, densely paleaceous; scales 1.2–2.5 × 0.3–0.5 mm, narrowly ovate, castaneous, shiny, stiff, paler brown basally, base cordate to auriculate, apex narrowly acuminate, filiform, margins sinuate to shortly dentate bearing short, glandular teeth, cells square to rectangular, arranged in longitudinal rows (Fig. 6A). Phyllopodia 3–5 mm long, swollen, dark brown, resinous, densely paleaceous as in rhizome; sterile fronds (6–)12–30(–42) cm; stipe (2–)4–12(–15) cm, 1–1.5 mm diam., stramineous, slightly canaliculate, often narrowly winged distally, when young bearing densely matted, pale rusty brown, scarious, lanceolate to deltoid scales 1–2 × 0.2–0.4 mm, base truncate to auriculate, the lobes prolonged into long, often bulbous-tipped cilia, apex long-acuminate, filiform, margins with long, spreading, usually paired cilia, cells rectangular; blade pendulous, narrowly to linear-elliptic, (4–)8–20(–30) × 1–2(–2.5) cm, base narrowly cuneate to long-attenuate, decurrent, apex acute to obtuse or rounded, subcoriaceous to coriaceous, costa rounded on both surfaces, stramineous, margins rounded, revolute, pale, veins indistinct, bifurcate, in part apically free, in part uniting into an intramarginal commissure, both surfaces of blade at first densely covered with arachnoid-tomentose layer of matted, pale reddish brown to buff-colored, deltate to rounded, hyaline scales 0.5–1 mm diam. (cilia included), base auriculate to sagittate, each lobe fringed with 3 to 5 long, spreading or crinkled, arachnoid hair teeth, apex filiform, margins bearing 1 to 2 pairs of long hair teeth and shorter teeth, cells toward base squarish to amoeboid, those to-

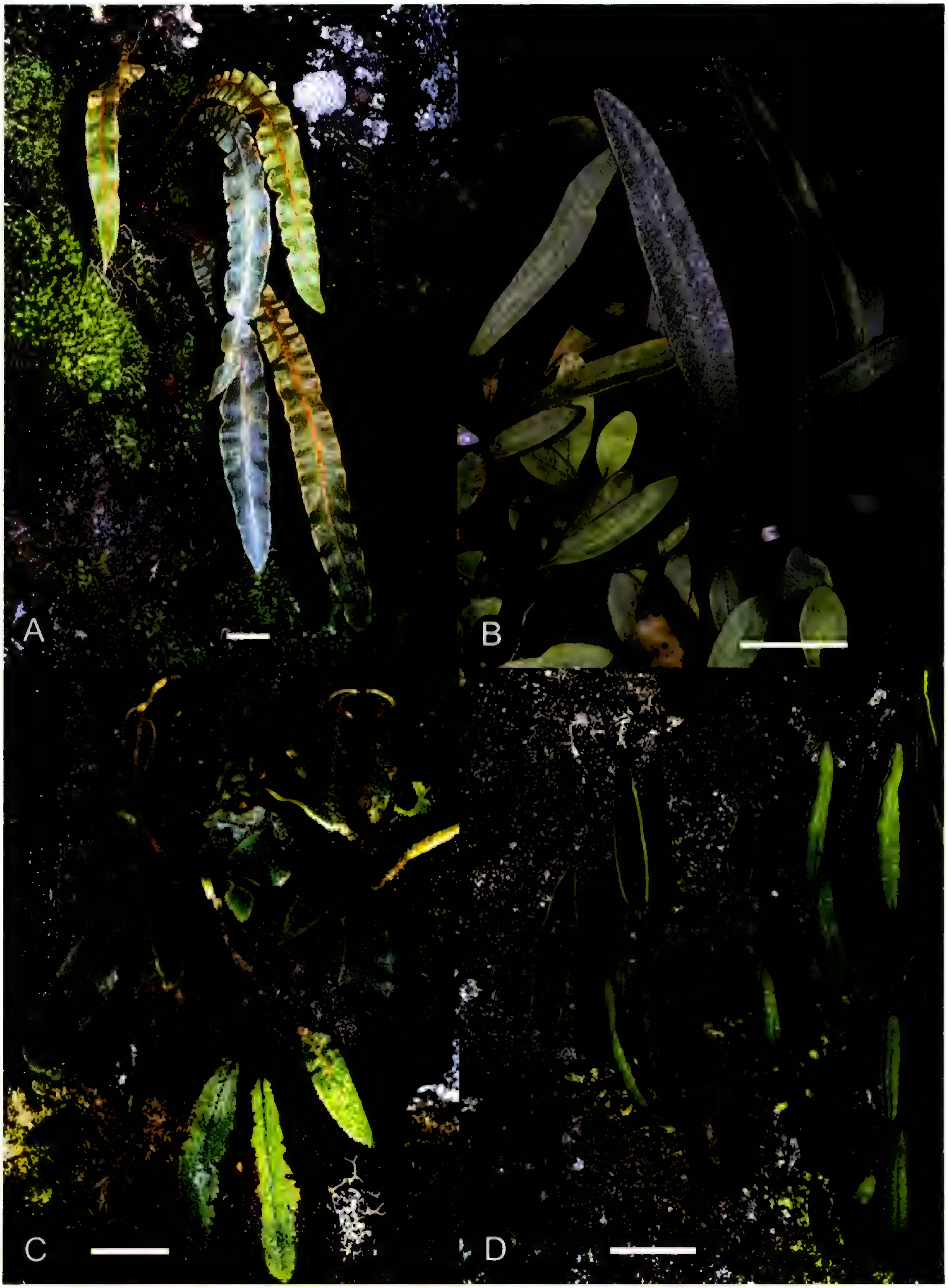


Figure 3. Habit of some Mascarene *Elaphoglossum* species. —A. *E. splendens* on mossy boulders from Réunion, same population as *Rouhan 218*. —B. Fronds of *E. lanatum*: some of them are densely covered with arachnoid-tomentose layer of matted, pale scales, becoming glabrescent, from Mauritius, *Rouhan et al. 192*. —C. *E. rufidulum* with fertile fronds, from Réunion, *Rouhan & Grangaud 224*. —D. *E. stipitatum* on rocks with fertile fronds, from Réunion, same population as *Rouhan 212*. Scale bars = 2 cm.

ward apex rectangular (Fig. 6B), adaxial blade surface glabrescent. Fertile frond (3–)8–14(–20) cm, slightly shorter than sterile frond; stipe slender, (2–)4–8(–11) cm; blade 5–7(–8.5) × 1–1.2(–1.4) cm, chartaceous, shape and scales of adaxial surface as in sterile frond. Spores 35–38 × 23–28 μm (excluding perispore), perispore cristate, crests 4–8 μm high, margins finely erose-dentate.

Distribution and habitat. Endemic to Mauritius, where it is restricted to nearly vertical river banks and cliff faces, often in sheltered overhangs growing on soil or decomposing lava rock at 300 to 800 m.

There is a *Bojer s.n.* sheet housed in K (not the sheet of the type) comprising three different specimens: the right-hand specimen is *E. lancifolium* and occurs in Réunion and Mauritius, but the two remaining specimens are *E. lanatum*, which is endemic to Mauritius. Consequently, the locality of Bourbon [Réunion] mentioned on the label of this sheet is probably erroneous or collections were mixed between both islands, because no other collections of *E. lanatum* are known from Réunion.

Discussion. The holotype of *Acrostichum viscosum* var. *lanatum, W. Bojer s.n* pro parte, includes 4 left-hand specimens only; the 2 remaining right-hand specimens are fertile fronds of *E. lancifolium* (Desv.) C. V. Morton (Lorence, 1976a: 199). *Elaphoglossum viscosum* (Sw.) J. Sm. is a species restricted to the Neotropics.

Extremely variable are frond size and shape, the degree to which the veins are free or unite intramarginally, and the percentage of aborted spores. This variability suggests a possible hybrid origin (Lorence, 1976a, 1984).

Although extremely variable, *E. lanatum* can be distinguished from all others in the Mascarenes by the blades with veins in part apically free, in part uniting into an intramarginal commissure, and by blades bearing an arachnoid-tomentose layer of matted, pale reddish brown, deltate to rounded, hyaline scales. Furthermore, it is unique in being the only Mauritian *Elaphoglossum* that is rupicolous and grows exclusively on vertical river banks and cliff faces composed of decaying lava.

In the Mascarenes, *Elaphoglossum lanatum* hybridizes with *E. hybridum* forming *E.* ×*setaceum*, and with *E. tomentosum* resulting in *E.* ×*adulterinum* (Lorence, 1984).

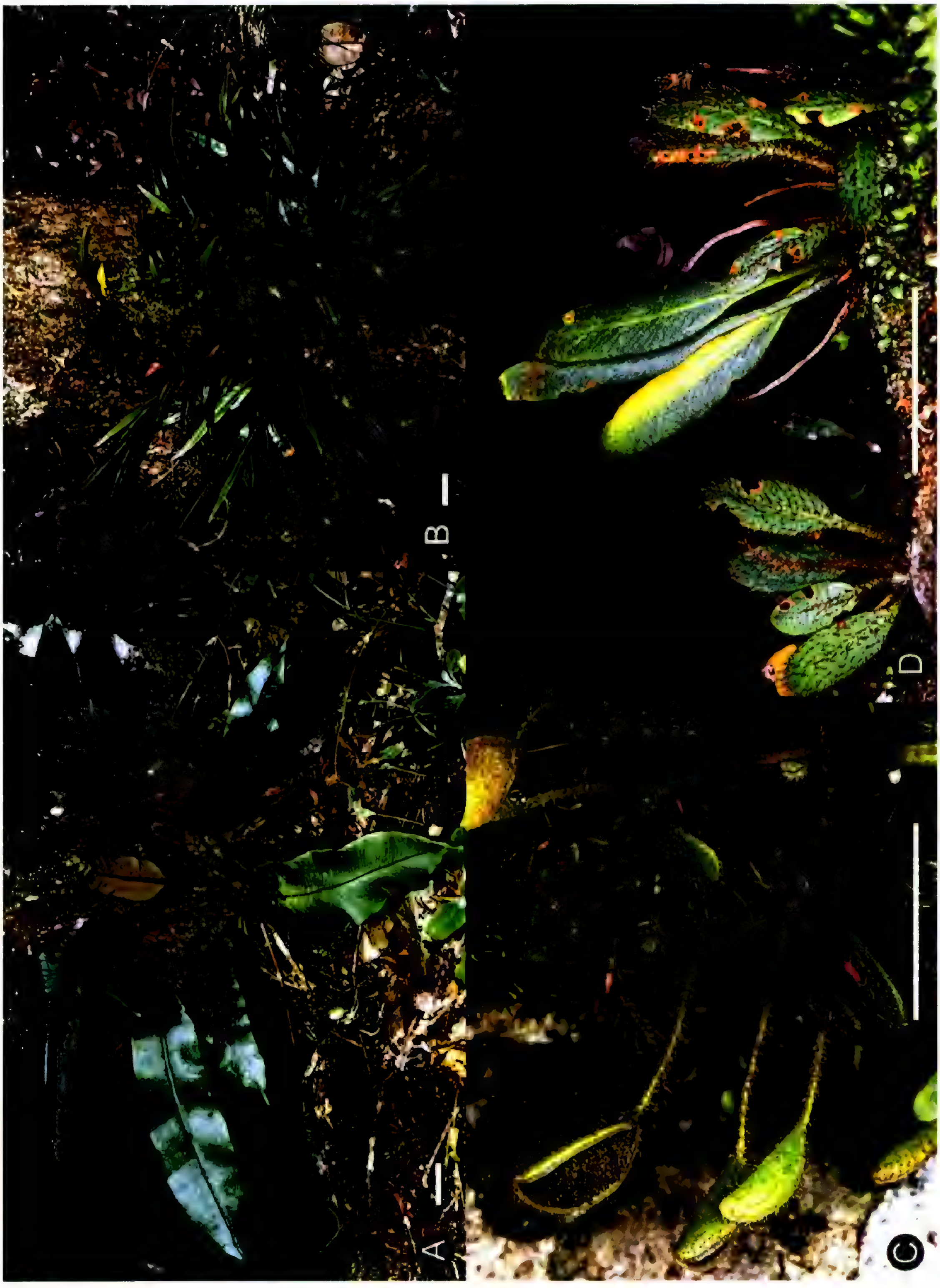
Selected specimens examined. MAURITIUS. Bel Ombre, *Lorence 1406* (MAU, MO); Black River Gorge, N edge behind Plaine Lièvre, *Lorence in MAU 15533* (MAU, MO, REU); Cascade 500 Pieds near Plaine Champagne, *Lorence 1173* (KRA, MAU, MO); Florin, le long de la Mare aux Riz, *Rouhan et al. 192* (MAU, NY, P, PTBG); Le Pouce Mtn., near summit, *Lorence 21.1 in MAU 16280* (MAU); Mare Longue Plateau, *Lorence in MAU 15243* (K, MAU, P, REU); Perrier Nat. Reserve, *Lorence 17.2 in MAU 15830* (MAU, MO); Bord de la rivière Cogliano, *Rouhan et al. 194* (MAU, NY, P [2], PTBG); Tamarind Falls Reservoir, *Lorence in MAU 15823* (MAU). RE-UNION? [Doubtful]. Without precise locality, *Bojer s.n.* (pro parte, left-hand and center collections, K).

11. Elaphoglossum lancifolium (Desv.) C. V. Morton, Contr. U.S. Natl. Herb. 38: 32. 1967.

Acrostichum lancifolium Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5: 310. 1811. TYPE: Mascareignes. 1801, *A. Du Petit-Thouars s.n.* (holotype, P-JU 1004!). Figure 4B.

Acrostichum salicifolium Willd. ex Kaulf., Enum. Filic. 58. 1824. *Elaphoglossum petiolatum* (Sw.) Urb. var. *salicifolium* (Willd. ex Kaulf.) C. Chr., Trans. Linn. Soc. London, Bot. 7: 421. 1912. *Elaphoglossum salicifolium* (Willd. ex Kaulf.) Alston, in Exell, Cat. Vasc. Pl. San Tomé 92. 1944. *Elaphoglossum petiolatum* (Sw.) Urb. subsp. *salicifolium* (Willd. ex Kaulf.) Schelpe, Contr. Bolus Herb. 1: 34. 1969. TYPE: Bourbon [Réunion]. *R. Desfontaines s.n.* pro parte, right-hand specimen only (holotype, B-W 19509!).

Fronds spaced 4–5 mm distant, borne in 2 ranks; rhizome short-creeping, 3–4 mm diam., sparsely branched, densely paleaceous, resinous; scales 3–5 × 0.5–0.8 mm, narrowly to linear-ovate, dark reddish brown, shiny, base truncate to cordate or auriculate, apex long-acuminate, filiform, margins entire except with a few short cilia and glands basally, cells fusiform. Phyllopodia 5–7 mm long, slightly swollen, blackish brown; sterile fronds 25–40(–44) cm; stipe 4–10(–23) cm, 1 mm diam., stramineous to reddish brown, slightly canaliculate, with scattered, substellate to elongate scales to 0.5–3.5 × 0.5–1 mm, margins with long hair teeth, stipe also with brown resinous punctations; blade linear-elliptic to linear, 20–30(–35) × 1–2(–2.5) cm, base narrowly cuneate to cuneate, sometimes decurrent, apex acute to long-acuminate, chartaceous to subcoriaceous, costa prominulous and rounded abaxially, canaliculate adaxially, margins revolute, veins prominulous, unbranched or bifurcate, apically free, tips thickened, dark, both surfaces of blade when young with sparse, scattered stellate scales 0.5–1 mm diam., pale brown, margins with usually 6 to 8 long hair teeth, scales denser along costa, blade surfaces also with scattered light brown, resinous punctations. Fertile frond equaling or slightly longer than sterile frond, 20–35(–40) cm; stipe slender, equaling to twice as long as sterile stipe; blade 14–26 × 0.7–1 cm, linear or linear-elliptic, base cuneate, apex acute, adaxial surface with scattered stellate scales. Spores 35–38 × 25–28 μm


A
B
C
D

(excluding perispore), perispore cristate, crests 3–5 μm high, margins entire to sinuate.

Distribution and habitat. Mauritius (300–800 m) and Réunion (100–1300 m); also Madagascar, Comoro Islands, Seychelles, San Tomé, and tropical Africa. Occurring in moist to wet forests in light to dense shade, epiphytic to 10 m above ground or growing on fallen trunks and mossy boulders.

Discussion. *Elaphoglossum lancifolium* resembles *E. richardii* by the blade shape but differs by its densely caespitose fronds and blade with free veins. *Elaphoglossum lancifolium* can be distinguished from all others by scales that are stellate with usually 6 to 8 long, straight hair teeth.

The type of *Acrostichum salicifolium, R. Desfontaines s.n.*, includes the right-hand specimen only. The remaining left-hand fertile specimen, an isolated fertile frond without rhizome, is of uncertain identity.

Acrostichum lancifolium Desv. is the oldest available name for the species (Morton, 1967: 32–33). Morton (1973: 215–216) further stated that *A. obductum* Kaulf. ex Spreng. (Syst. Veg. (ed. 16): 34. 1827) is a superfluous name based on the same type as *A. lancifolium* Desv.: "It is likely that Kaulfuss intended his *A. obductum* to be based on Mauritius, *Sieber*, Syn. Fil. no. 25 [referring now to *E. tomentosum* (Bory ex Willd.) H. Christ], and it has been perhaps generally so considered, although never definitely lectotypified. But when Sprengel published the name he did not mention Sieber or indeed cite any specimens, merely citing [erroneously] *Acrostichum lancifolium* Desv. as a synonym. Since the name *A. lancifolium* was a legitimate and available name, there was no need to propose a different name, *A. obductum* . . . and so by Art. 63 [modern equivalent in the ICBN, Greuter et al., 2000: Art. 52] of the *Code* the name *A. obductum* must be considered superfluous, and by Art. 7 [7.5] it must be typified on the basis of the name that ought to have been adopted, thus on the type of *A. lancifolium.*" Consequently, the name *Acrostcihum obductum* or its combination *Elaphoglossum obductum* (Kaulf. ex Spreng.) T. Moore (Index Fil.: 124. 1857), has been widely misapplied. *Elaphoglossum tomentosum* is indeed the correct name for the plant identified by almost all authors as *Acrostichum* (*Elaphoglossum*) *obductum* sensu Kaulfuss (even if never published by Kaulfuss himself), which is different from *Acrostichum* (*Elaphoglossum*) *obductum* sensu Kaulfuss ex Spreng., because according to the *Code* the latter name is illegitimate and must now refer to *Elaphoglossum lancifolium.* The following misapplied name found in the early Mascarene literature should refer to *E. lancifolium*: *Acrostichum viscosum* sensu Bojer, Hortus Maurit. 412. 1837, sensu Baker, Fl. Mauritius 512. 1877, sensu Cordem., Fl. Réunion, part 1: 83. 1891, Fl. Réunion 94. 1895, non *Acrostichum viscosum* Sw., Syn. 10: 193. 1806. *Elaphoglossum viscosum* (Sw.) J. Sm. is a Neotropical species.

Selected specimens examined. MAURITIUS. Bassin Blanc, *Lorence 506* (MO); Bel Ombre, N of Bon Courage forest station, *Lorence & Florens 7017* (MAU, PTBG); Bois Sec near Grand Bassin (date?), *Lorence s.n.* (MO); Curepipe, Kanaka, *Bijoux 69 in MAU 2570* (MAU); Les Mares, *Rochecouste & Orian s.n.* (MAU); Macabé, Réserve de Brise Fer, *Rouhan et al. 187* (MAU, P); Macabé, sentier menant à la Mare aux Joncs, *Rouhan et al. 181* (MAU, P); Mare Longue Plateau, Mare Longue–Macabé rd., *Lorence 7.3 in MAU 15813* (K, MAU, M, MO, P, REU); Mt. Lagrave, E flank, *Lorence 792 in MAU 16315* (MAU); Perrier Nat. Reserve, *Rouhan et al. 193* (MAU, P); Pétrin Nat. Reserve, *Lorence 8.5* (MO); Piton du Fouge, *Lorence 318* (MO); Piton du Milieu, *Lorence 10.3* (K, MAU, MO, P); Piton Grand Bassin, *Julien in MAU 14594* (MAU); Plaine Paul, *Vaughan in MAU 12544* (MAU); Rivière Cogliano near Mare aux Vacoas, *Lorence 1374* (MO); Rivière des Galets, below Cascade 500 Pieds, *Lorence 1479* (KRA, M, MAU, MO). RÉUNION. Bois Blanc, *Guého in MAU 15362* (MAU); Cascade de Bras Rouge, *Rouhan 236* (NY, P, PTBG); Cilaos, au dessus des Thermes, *Cadet 4127* (REU); Dimitile, *Rouhan & Grangaud 201* (NY, P); Forêt du Grand Brûlé, *Cadet 319 bis* (P); Grande Jument, *Rouhan & Grangaud 197* (P); Hauts des Trembles, *Bosser 20624* (P); Morne des Patates Durand, *Lorence in MAU 15628* (MAU); St. Philippe, forêt de Mare Longue, *Guého in MAU 15303* (MAU); St. Philippe, Mare Longue, *Schlieben 10928 in MAU 12416* (MAU); Tremblet, *Rouhan & Grangaud 210* (NY, P, PTBG); Vallée de Langevin a Grand Galet, *Cadet 3718* (REU).

12. Elaphoglossum lepervanchei (Bory ex Fée) T. Moore, Index Fil.: 11. 1857. *Acrostichum lepervanchei* Bory ex Fée, Mém. Foug., 2: 37, tab. 9(1). 1844 [1845]. TYPE: Réunion. *S.n.*, [Hb. Bory 27,14] pro parte, right-hand specimen only (lectotype, designated by Lorence (1976: 200), P!). Figure 2B.

Elaphoglossum didynamum (Fée) T. Moore, Index Fil.: 8. 1857. *Acrostichum didynamum* Fée, Mém. Foug., 2:

←

Figure 4. Habit of some Mascarene *Elaphoglossum* species. —A. Epiphyte at the base of a trunk, *E. hybridum* with a fertile frond, from Réunion, same population as *Rouhan et al. 228.* —B. *E. lancifolium*, from Mauritius, *Rouhan et al. 187.* C, D. *E. spatulatum* on mossy boulders, from Réunion, *Rouhan & Grangaud 246.* —C. Shows the longer fertile fronds, conduplicate before maturity. —D. Sterile fronds. Scale bars = 2 cm.

37, tab. 16(2). 1844 [1845]. TYPE: Réunion. *P. Lépervanche-Mézières s.n.* [Hb. Bory 27, 13] (holotype, P!).

Elaphoglossum curtisii (Baker) C. Chr., Index Fil.: 305. 1905. *Acrostichum curtisii* Baker, Ann. Bot. 5: 489. 1891. TYPE: Madagascar. 1881, *C. Curtis 121* (holotype, K!; photo of holotype, P!).

Elaphoglossum borbonicum (Baker) C. Chr., Index Fil.: 303. 1905. *Acrostichum borbonicum* Baker, Ann. Bot. 5: 491. 1891. TYPE: Bourbon [Réunion]. *I. B. Balfour 27* (holotype, K!).

Fronds spaced (2–)8–12(–25) mm, 2-ranked; rhizome moderately long-creeping, 3–5 mm diam., occasionally branched, densely paleaceous near apex; scales 4–10 × 0.5–1 mm, narrowly ovate, elliptic or linear, thin, pale yellowish to reddish brown, base truncate to auriculate, apex filiform with bulbous tip, margins involute, bearing especially toward base long, flexible gland-tipped cilia, the cells thin-walled, rectangular to fusiform, alternating with bands of shorter, squarish cells (Fig. 5D). Phyllopodia 15–25 mm long, slightly swollen, articulated, dark brown to black, paleaceous; sterile fronds 7–35(–60) cm; stipe 2–15(–30) cm × 1–2 mm, stramineous to rusty brown, slightly canaliculate, narrowly winged in distal 0.5–0.7, sparsely paleaceous, the scales loose, pale brown 1–2 mm, margins ciliate; blade narrowly ovate-elliptic to linear-elliptic or narrowly obovate, 5–20(–26) × 1.5–4.5(–9) cm, base narrowly to broadly cuneate or truncate, usually attenuate and decurrent, apex obtuse to acuminate, subcoriaceous to coriaceous, costa prominulous, rounded abaxially, flattened to canaliculate adaxially, margins thin, revolute, veins distinct, prominulous, bifurcate 1 to 2 times, apically free, tips thickened, adaxial surface of blade glabrate, abaxial surface of blade with scattered, appressed dark brown scales 0.2–0.5 mm diam., irregularly stellate with bulbous-tipped cilia (Fig. 5E), scales larger and denser along costa. Fertile frond 12–35(–45) cm long; stipe 1.5 to 3 times longer than in sterile frond; blade narrowly elliptic to linear-elliptic, 6–20(–36) × 1.2–2.6(–4) cm, flexible, apex acute to obtuse, base cuneate to attenuate, slightly decurrent, veins visible adaxially. Spores 35–38 × 23–26 μm (excluding perispore), the perispore cristate, crisped, 4–10 μm wide with erose-dentate margins.

Distribution and habitat. Mauritius and Réunion; also Madagascar, Comoro Islands, and the Seychelles. This species occurs in humid localities from low to middle elevations, 200 to 900 m on Mauritius and 160 to 1300 m on Réunion. One of the most common Mascarene *Elaphoglossum* species, it abounds in ericoid shrubland and low, open *Sideroxylon* L. forests where it occurs terrestrially or at bases of trees and shrubs. It is rarely found in tall, shady wet forests.

Discussion. *Elaphoglossum lepervanchei* is extremely variable in size and shape of fronds, even on a single plant. This has resulted in a proliferation of synonyms and misapplied names in the literature. This species resembles *E. macropodium* by frond shape and reddish brown rhizome scales, but can be distinguished by having free veins, thinner rhizomes, and smaller rhizome scales with crisped, involute, glandular-ciliate margins.

On Mauritius, *E.* ×*revaughanii* is a natural hybrid between *E. lepervanchei* and *E. sieberi* (Lorence, 1984).

The specific epithet was originally published as "*lepervanchii.*" Since the species was dedicated to Mr. Lépervanche, the publication is valid according to the *Code* (Art. 32.6; Greuter et al., 2000), but the Latin termination contrary to Rec. 60C.1 is treated as an orthographic error to be corrected (Art. 60.11). Therefore, the correct spelling of the name is "*lepervanchei.*"

In the literature concerning the Madagascan and Mascarenes area, the following misapplied names should actually refer to *E. lepervanchei*:

Acrostichum conforme sensu Bojer, Hortus Maurit. 412. 1837; sensu Baker, Fl. Mauritius 511. 1877; sensu Cordem., Fl. Réunion, part 1: 81. 1891, Fl. Réunion 93. 1895, non *Acrostichum conforme* Sw., Syn. Fil. (Sw.) 10, 192, tab.1(1). 1806.

Acrostichum ovalifolium Bojer, Hortus Maurit. 412. 1837, nom. nud.

Acrostichum latifolium sensu Baker, Fl. Mauritius 511. 1877, non *Acrostichum latifolium* Sw., Prodr. Pl. Ind. Occid.: 128. 1788.

Elaphoglossum latifolium sensu C. Chr., Trans. Linn. Soc. London, Bot. 7: 420. 1912, non *Elaphoglossum latifolium* (Sw.) J. Sm., J. Bot. 1: 197. 1842.

Elaphoglossum conforme sensu C. Chr., Trans. Linn. Soc. London, Bot. 7: 420. 1912; sensu Tardieu in Humbert, Fl. Madagasc. 5(2): 35. 1960, non *Elaphoglossum conforme* (Sw.) J. Sm., J. Bot. 4(27): 148. 1841.

Selected specimens examined. MAURITIUS. Alexandra Falls, *Rouhan et al. 175* (MAU, NY, P); Bassin Blanc, *Lorence 828 in MAU 16319* (MAU); Bassin Blanc to Les Mares path, *Lorence in MAU 14610* (MAU); Bel Ombre, *Lorence 327* (MO); Black River Gorges from Plaine Champagne, *Lorence in MAU 14880* (K, MAU, P); Chamarel rd. from Plaine Champagne, *Lorence in MAU 14640* (MAU); Crown Land Declerc, *Julien in MAU 13318* (MAU); Macabé to Brise Fer rd., *Lorence in MAU 14588* (MAU); Mare Longue Plateau, rd. to Macabé, *Lorence in MAU 15242* (MAU, REU), *Rouhan et al. 188* (MAU, P, PTBG); Pétrin Nat. Reserve, rd. to Grand Bassin, *Lorence 12.1 in MAU 15822* (K, MAU, P, REU), *Lorence 18.3 in MAU 15812* (K, MAU, MO, P, REU); Pétrin to Macabé rd., *Vaughan in MAU 12551* (MAU, P); Piton Brise Fer, *Lorence 3.1 in MAU* (K, M, MAU, MO, P); Piton du Fouge, *Lorence 1626* (MO); Piton Grand Bassin, *Lorence in MAU 14589* (MAU); Plaine Champagne to Chamarel rd., *Lorence 14.1 in MAU*

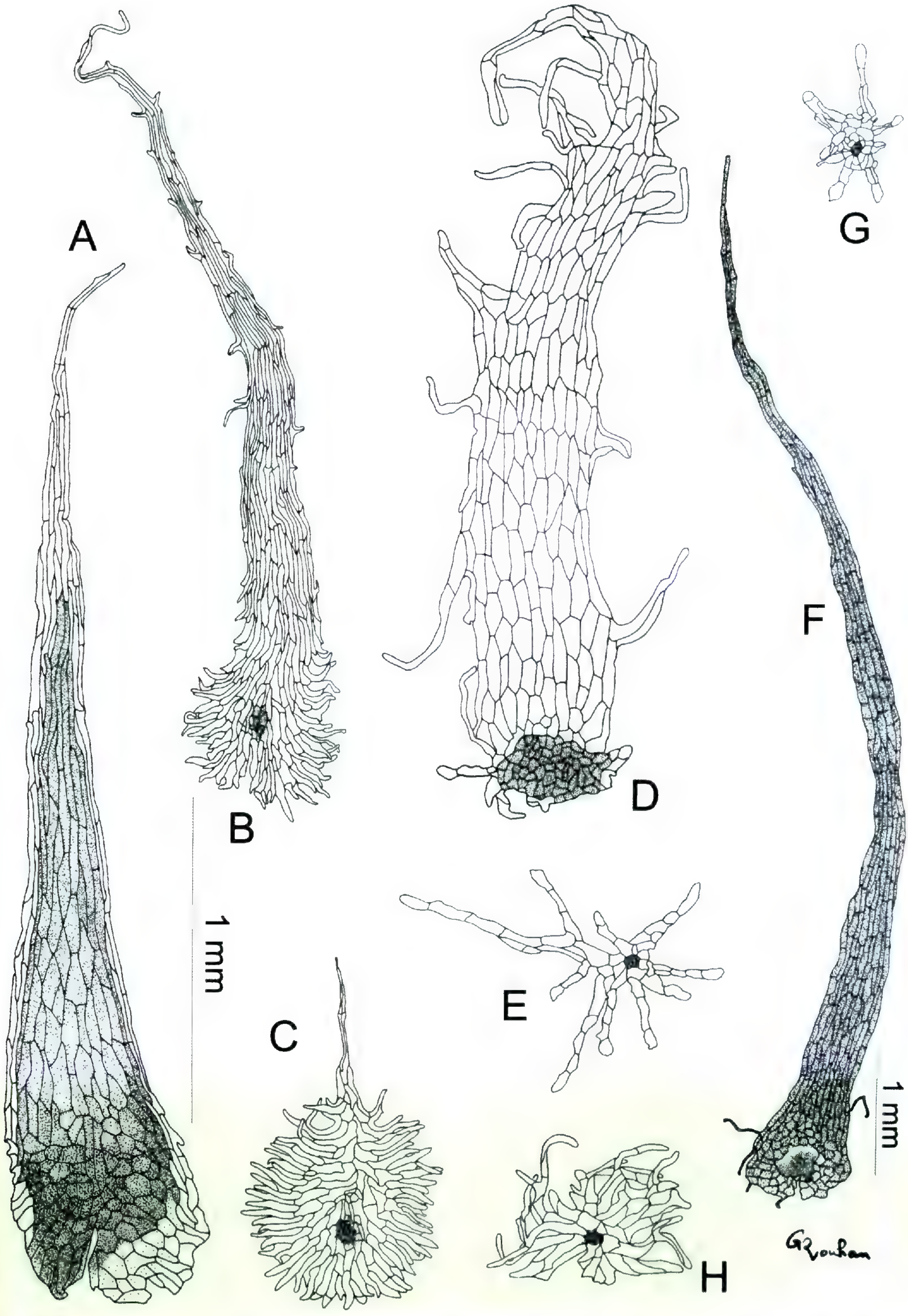


Figure 5. Scales of some Mascarene *Elaphoglossum* species. A–C. *E. heterolepis*, from Réunion, Plaine des Fougères, *Boivin s.n.* —A. Rhizome scale. —B, C. Lamina scales. D, E. *E. lepervanchei*, from Mauritius, *Lorence M255.* —D. Rhizome scale. —E. Lamina scale. F, G. *E. sieberi*, from Mauritius, *Lorence 15016.* —F. Rhizome scale (own scale bar). —G. Lamina scale. —H. Lamina scale of *E. tomentosum*, from Mauritius, *Lorence 1092.* Scale bar = 1 mm, except separate scale in F.

15811 (K, KRA, MAU, MO, P, REU); Plaine Champagne, S of Black River Gorges, *Lorence in MAU 15010* (K, MAU, P); Plaine Champagne, S of Plaine Paul, *Lorence 2.3 in MAU 15831* (MAU, MO). RÉUNION. Brûlé, *Bédier 52* (pro parte, right-hand specimen P); Cilaos, au dessus des Thermes, *Cadet 4130* (REU); Forêt du Bébour, *Lorence in MAU 15642* (MAU, MO); sentier de la rivière, *Rouhan & Grangaud 248* (NY, P, PTBG); Petite Plaine des Palmistes, *Cadet 4017* (REU); Plaine des Fougères, *Rouhan et al. 227* (P); Tremblet, *Rouhan & Grangaud 208* (NY, P, PTBG); Valleé de Langevin, *Cadet 3766* (REU).

13. Elaphoglossum macropodium (Fée) T. Moore, Index Fil.: 11. 1857. *Acrostichum macropodium* Fée, Mém. Foug., 2.: 30, tab. 6(2). 1844 [1845]. TYPE: Bourbon [Réunion]. 1844, *s.n.*, [Hb. Bory 30, 12] (holotype, P!). Figure 2D.

Acrostichum conforme Sw. var. *carmichaelii* Baker, Fl. Mauritius: 511. 1877. TYPE: Mauritius. *D. Carmichael s.n.* (holotype, K! [Hb. Hook.]).

Fronds densely caespitose, borne in 2 ranks; rhizome short-creeping, thick, 10–15 mm diam., unbranched, densely paleaceous; scales narrowly ovate, (10–)15–25 × 2–4 mm, reddish to yellowish brown, flat, thin, truncate to cordate at base, acute at apex, margins bearing rare bulbous-tipped cilia, cells linear to fusiform in vertical rows, thin-walled. Phyllopodia 1–1.5 cm long, swollen, brown to dark brown, densely paleaceous; sterile fronds 30–55(–73) cm; stipe 8–20(–24) cm × 3–4 mm, stramineous, adaxially canaliculate, narrowly winged distally, bearing scattered appressed scales; blade narrowly elliptic to ovate- or oblong-elliptic, 18–36(–50) × 4–6.5(–8.6) cm, base narrowly to broadly cuneate, decurrent, apex acute to short-acuminate, coriaceous, costa prominulous, rounded abaxially, slightly canaliculate adaxially, margins revolute, veins distinct, prominulous on both surfaces, bifurcate 1 to 2 times, uniting apically into an intramarginal commissure, adaxial surface of blade glabrate, abaxial surface of blade with sparse, scattered appressed brown scales 0.5 mm diam., stellate with bulbous-tipped cilia, scales larger and denser on abaxial surface of costa. Fertile frond 30–55 cm, equaling sterile, stipe equaling or slightly longer than in sterile frond; blade narrowly elliptic, 5–12(–15) × 2–4 cm, base narrowly to broadly cuneate, apex acute to rounded. Spores 33–38 × 28–30 μm (excluding perispore), the perispore cristate, the crests 4–10 μm high with finely spinulose-denticulate margins.

Distribution and habitat. Mauritius and Réunion; also tropical eastern and southern Africa, Seychelles, and Comoro Islands. Common and widespread in Réunion as an epiphyte on mossy trunks up to 10 m above ground or rarely terrestrial, in shade of wet forests and ericoid shrublands from 100 to 1500 m. *Elaphoglossum macropodium* has not been collected in Mauritius since 1923 and is either extremely rare or extirpated there [vs. Réunion].

Discussion. *Elaphoglossum macropodium* resembles *E. sieberi* by the frond shape and dimensions, and it resembles *E. lepervanchei* by frond shape and reddish brown rhizome scales. *Elaphoglossum macropodium* differs from *E. sieberi* and *E. lepervanchei* by its extremely thick rhizomes (10–15 mm diam.) densely clothed with larger, flat, thin, subentire reddish to yellowish brown scales.

The following name was misapplied by Cordemoy and should now refer to *E. macropodium*: *Acrostichum sieberi* sensu Cordem., Fl. Réunion, part 1: 81. 1891, Fl. Réunion 93. 1895, non *Elaphoglossum sieberi* Hook. & Grev, Icon. Filic. tab. 237. 1831.

Selected specimens examined. MAURITIUS. Curepipe, Kanaka, *Bijoux 73* (P); Savanne, Nov. 1923, *s.n.* (pro parte, left-hand collection, MAU). RÉUNION. Bébour, *Lorence in MAU 15638* (MAU [2], MO); Brûlé, *Bédier 54* (P [2]); Saint-Philippe, *Bosser 9559* (P, [2]); Montée de la Plaine des Affouches, *Bosser 20432* (P); Morne des Patates Durand, *Lorence in MAU 15620* (MAU); Plaine des Chicots, sentier Dos d'Ane, *Bosser 22485* (P); Salazie, 1835, *Lépervanche-Mézières s.n.* [Hb. Bory 30,10] (P); Forêt du Grand Brûlé, *Cadet 317* (P); Grand Bénard, *Boivin 802* (P); Dimitile, *Rouhan & Grangaud 207* (NY, P, PTBG); Tremblet, *Rouhan & Grangaud 209* (NY, P); Plaine des Fougères, *Rouhan et al. 232* (P), Aug. 1850, *Boivin s.n.* (P).

14. Elaphoglossum ×revaughanii Lorence [*Elaphoglossum lepervanchei* (Bory ex Fée) T. Moore × *E. sieberi* (Hook. & Grev.) T. Moore], Fern Gaz. 12: 342, fig. 1. 1984. TYPE: Mauritius. Mare Longue Plateau, 1973, *D. H. Lorence 14.3* (holotype, MAU 15818!; isotypes, K!, MAU!, MEXU!, MO!, P!, REU!).

Fronds caespitose, borne in 2 ranks; rhizome short-creeping, 5–6 mm diam., occasionally branched, densely paleaceous; scales 3–6 × 0.5–0.8 mm, narrowly ovate to lanceolate, black, shiny, rigid, base truncate to cordate or auriculate with short, glandular cilia, apex long-acute, filiform, margins entire or rarely with a few long, glandular cilia, the cells small, rectangular, seriate, black and opaque. Phyllopodia 15–20 mm long, slightly swollen, grayish to yellowish brown, paleaceous; sterile fronds (30–)44–53 cm; stipe 14–16(–19) cm × 2–2.6 mm, stramineous, canaliculate, when young bearing scattered dark brown to black, appressed-ovate to lanceolate scales 0.5–4 × 0.2–0.5 mm, base cordate to auriculate, fringed by short glandular cilia, apex filiform, sinuate, margins sinuate

with scattered glandular cilia, cells dark brown; blade narrowly elliptic to linear-elliptic, (19–)30–35 × (4.3–)5.5–7 cm, base narrowly cuneate, decurrent along distal 0.25–0.3 of stipe, apex acute to acuminate, subcoriaceous, costa prominulous and rounded abaxially, canaliculate adaxially, margins revolute, veins visible, raised, bifurcate 1 to 2 times, in part apically free and with thickened tips, in part uniting into intramarginal arcs, both surfaces of blade glabrate except for scattered brown, glandular-ciliate scales 0.5 mm diam. along abaxial surface of costa. Fertile frond (30–)35–42 cm long; stipe (15–)17–22 cm; blade narrowly elliptic to linear-elliptic, 15–23 × 1.5–2.6 cm, apex acute to acuminate, base narrowly cuneate, adaxial surface pallid with minute, scattered scales, veins not visible. Spores: 4%–5% very large (75–88 × 50–60 µm, excluding perispore), 65%–67% aborted, 29%–30% normal (40–50 × 30–35 µm, excluding perispore), the perispore with large, ruffled crests 10–15 µm high.

Distribution and habitat. Mauritius, endemic and known only from Mare Longue Plateau (630 m) and Pétrin Nature Reserve (660 m).

Discussion. This natural hybrid between *E. lepervanchei* and *E. sieberi* possesses a high percentage of aborted or abnormal spores and presents morphological characters intermediate between these two species. *Elaphoglossum* ×*revaughanii* has veins partly free (as in *E. lepervanchei*) and partly reunited into a submarginal commissure (as in *E. sieberi*), and scales on the lower portion of the stipe and phyllopodium are intermediate between those of both parents. The hybrid is more robust than either parent, which both occur in the same biotope, usually as depauperate individuals growing at the bases of stunted trees and shrubs because it is a marginal, suboptimal habitat for these shade-loving, wet forest epiphytes. Obviously more successful than either parent in this particular ecological setting of low shrub vegetation, the hybrid behaves like a terrestrial heliophilous or hemisciophilous species and apparently reproduces vegetatively by rhizome branching (Lorence, 1984).

Specimens examined. MAURITIUS. Mare Longue Plateau, *Lorence 11.1* (MAU, MEXU, MO), *Lorence 8.6 in MAU 15531* (K, MAU, MO, P, REU), *Lorence 1176* (MO), *Rouhan et al. 190* (MAU, NY, P [2], PTBG); Pétrin Nat. Reserve, *Lorence 1497* (MAU, MO).

15. Elaphoglossum richardii (Bory ex Fée) H. Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. 36(1): 35. 1899. *Aconiopteris richardii* Bory ex Fée, Mém. Foug., 2: 80, tab. 16(4). 1844 [1845]. *Acrostichum richardii* (Bory ex Fée) Hook., Sp. Fil. 256. 1864. TYPE: Bourbon [Réunion]. "Dans les forêts sur les vieux bois," *J. M. C. Richard 10* [Hb. Bory 30,28] (holotype, P!). Figure 1C.

Fronds spaced 1–2 cm distant, borne in 2 ranks; rhizome long-creeping, 2–3.5 mm diam., unbranched, paleaceous, resinous; scales 3–6 × 0.3–0.5 mm, linear-ovate to lanceolate, sinuate, brown to dark brown, shiny, thin, base cordate, apex long-acute, margins bearing short cilia or reflexed teeth toward base, cells small, oblong-fusiform (Fig. 6C). Phyllopodia 10–15 mm long, slightly swollen, dark brown; sterile fronds 25–40(–55) cm; stipe 6–12(–15) cm, 1–2 mm diam., stramineous to brown, when young bearing minute, brown resinous punctations and abundant, ovate to oblong scales to 5 × 0.4 mm with glandular ciliate-dentate margins; blade linear-elliptic, 15–34 × 1.5–2(–3) cm, base narrowly cuneate, often decurrent, apex acute to obtuse, subcoriaceous, costa prominulous and rounded abaxially, canaliculate adaxially, margins revolute, veins distinct, bifurcate, apically uniting into an intramarginal commissure, both surfaces of blade minutely paleaceous when young, scales ovate-triangular to linear-oblong, 0.5–1 × 0.2–0.3 mm, pale brown, scarious, margins with hair teeth, with cluster of resiniferous glands at base (Fig. 6D), adaxial surface glabrescent leaving brown resinous punctations. Fertile frond equaling or slightly longer than sterile frond; stipe slender, equaling or slightly longer than sterile stipe; blade 11–24 × 0.8–1.4 cm, linear, base narrowly cuneate, decurrent, apex acute, adaxial surface paleaceous and with resinous punctations. Spores 30–33 × 23–25 µm (excluding perispore), perispore cristate, crests 2.5–5 µm high, margins finely sinuous-erose.

Distribution and habitat. Réunion, endemic. Epiphytic on mossy trees and boulders up to 3 m above ground level in shady wet forests, 300 to 1460 m.

Discussion. The specific epithet was published as "*richardi.*" Since the species was dedicated to Mr. Richard, the publication is valid according to the *Code* (Art. 32.6; Greuter et al., 2000), but the Latin termination contrary to Rec. 60C.1 is treated as an orthographic error to be corrected (Art. 60.11). Therefore, the correct spelling of the name is "*richardii.*"

This species resembles *Elaphoglossum lancifolium* by the blade shape, but differs by more widely spaced fronds, blades with non-stellate scales, and veins uniting apically to form a submarginal commissure. In addition to the latter character, *E. richardii* can be distinguished by linear-elliptic

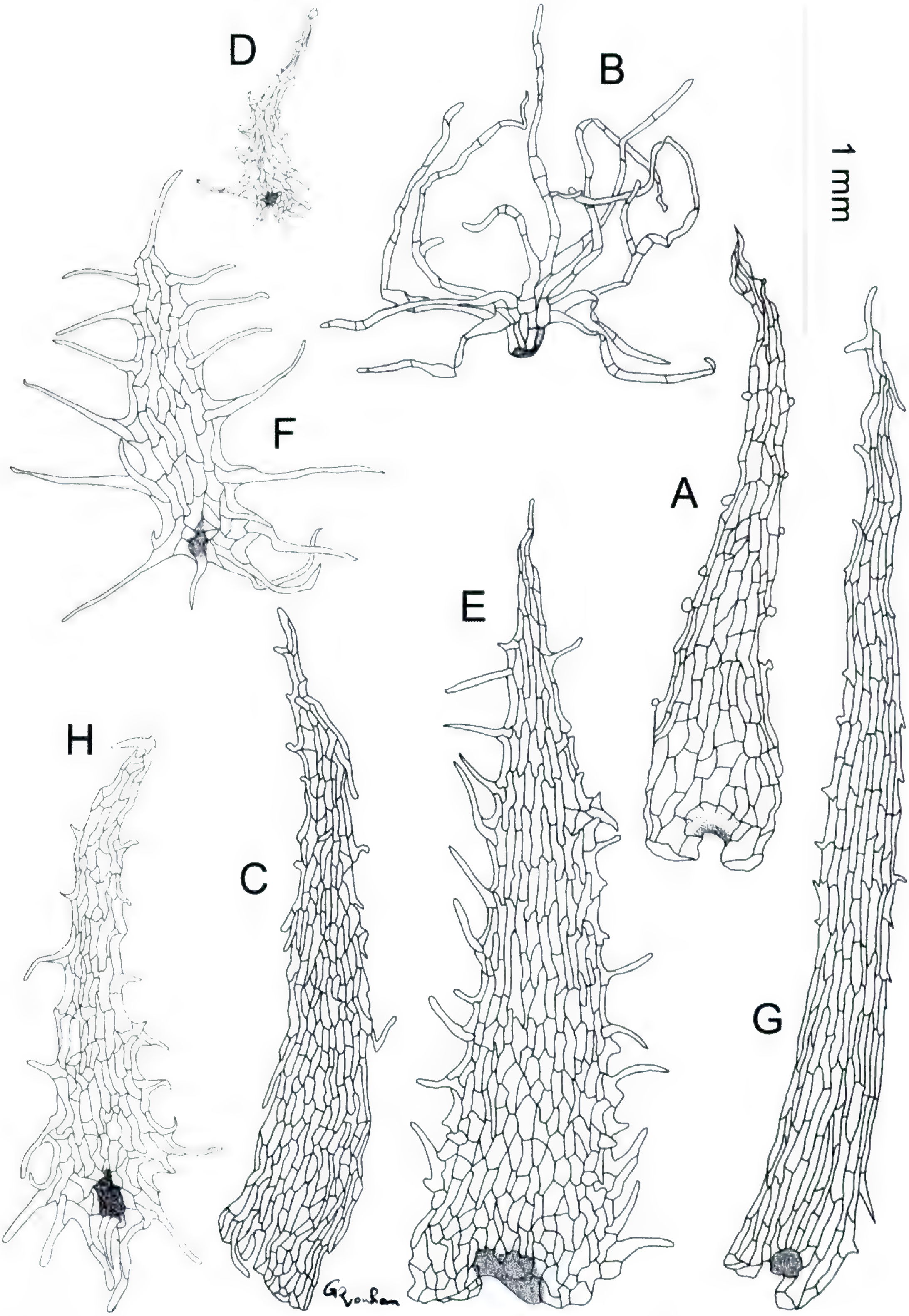


Figure 6. Scales of some Mascarene endemic *Elaphoglossum* species. A, B. *E. lanatum*, from Mauritius, *Lorence 15014*. —A. Rhizome scale. —B. Lamina scale. C, D. *E. richardii*, from Réunion, *Lorence 15647*. —C. Rhizome scale. —D. Lamina scale. E, F. *E. splendens*, from Réunion, *Bory 42* [Hb. Bory 27,28]. —E. Rhizome scale. —F. Lamina scale. G, H. *E. stipitatum*, from Réunion, *Cadet 2048*. —G. Rhizome scale. —H. Lamina scale. Scale bar = 1 mm.

blades (1.5–2 cm wide), paleaceous when young and bearing resinous punctations. The following name misapplied by Tardieu should refer to *E. richardii*: *Elaphoglossum stipitatum* sensu Tardieu, Notul. Syst. 15(4): 429, pl. 2, figs. 1–3. 1959, non *Elaphoglossum stipitatum* (Bory ex Fée) T. Moore, Index Fil.: 15. 1857.

Selected specimens examined. RÉUNION. Basse Vallée, Ravine Pérote, *Rouhan 234* (P); Bébour forest, *Lorence in MAU 15644* (MAU, MO); Bois des Hauts de Saint-Paul, *s.n. 75* (P [2]); Boucan Launay, 1852, *Bernier s.n.* (P); Brûlé, *Bédier 56* (P), *57* (P); Chemin Arnoux, *Cadet 879* (P); Hauts de l'Ouest, sentier de l'îlet Alcide, *Rouhan et al. 244* (P); Hauts de St. Rose (Forêt Mourouvin), *Cadet 3884* (P, REU); Le Dimitile, *Rouhan & Grangaud 205* (NY, P, PTBG); Mare Longue forest, *Lorence in MAU 15630* (MAU); Morne des Patates Durand, *Lorence in MAU 15647* (MAU, MO, P); Plaine des Fougères, *Rouhan et al. 231* (NY, P, PTBG); Plaine des Palmistes, June 1851, *Boivin s.n.* (P).

16. Elaphoglossum rufidulum (Willd. ex Kuhn) C. Chr., Index Filic.: 314. 1905. *Acrostichum rufidulum* Willd. ex Kuhn, Filic. Afr. 47. 1868. *Elaphoglossum deckenii* (Kuhn) C. Chr. var. *rufidulum* (Willd. ex Kuhn) Tardieu, Notul. Syst. 15(4): 430, pl. 4, figs. 6–10. 1959. *Elaphoglossum hirtum* (Sw.) C. Chr. var. *rufidulum* (Willd. ex Kuhn) C. Chr., Dansk. Bot. Ark. 7: 170. 1932. TYPE: Madagascar. *J-B. Lamark s.n.* (holotype, B-W 19511; B-W microfiche MO!). Figure 3C.

Fronds densely caespitose, borne in 2 to 3 ranks; rhizome very short-creeping, 3 mm diam., unbranched, densely paleaceous; scales 2–3 × 1 mm, narrowly ovate, dark brown, shiny, paler basally, base cordate to auriculate, apex acute, margins subentire or bearing black hair teeth 0.1–0.3 mm long, cells rectangular to fusiform with thick walls. Phyllopodia 0.6–1 cm long, slightly swollen, dark brown, densely paleaceous as in rhizome, but scales with long marginal cilia; sterile fronds 23–34 cm; stipe 9–15 cm, 1 mm diam., stramineous, canaliculate, densely paleaceous, the scales spreading, pale brown to reddish brown, narrowly ovate, 3–4 × 0.5–1.2 mm, base cordate to auriculate, apex acute, margins bearing pale brown to black hair teeth 0.2–0.8 mm long, cells rectangular to oblong-fusiform, often bifurcate apically; blade narrowly elliptic, 13–19 × 2–2.5 cm, base narrowly cuneate, apex short- to long-acuminate, chartaceous, costa prominulous and rounded on both surfaces, margins rounded, weakly revolute, margins and costa bearing many, reddish brown, spreading, ovate scales 1–3 × 0.2–0.5 mm, base auriculate, apex acute, margins bearing 2 to 8 pairs of stiff, long hair teeth, veins prominulous, simple or bifurcate, apically free, both surfaces of blade covered with numerous reddish brown spreading or imbricated scales similar to those on margins but smaller. Fertile frond about as long as sterile frond; stipe longer than sterile stipe, ca. 18 cm; blade ca. 10 × 1.3 cm, narrowly elliptic, base narrowly cuneate, apex obtuse, rounded, scales of adaxial blade surface and both surfaces of costa as in sterile frond. Spores 37–38 × 28–30 μm (excluding perispore), perispore cristate, crests 2.5–5 μm high, margins finely sinuate-dentate.

Distribution and habitat. Réunion and Madagascar. This species is rare on Réunion, where it occurs on lava in the shade of fissures and grottos in ericoid vegetation from 2200 to 2340 m.

Discussion. Elaphoglossum rufidulum resembles *E. splendens* in general appearance and by its rhizome and frond scales with stiff hair teeth, but *E. rufidulum* occurs at higher elevations, and its sterile fronds are less densely paleaceous, with the imbricated scales not completely obscuring the frond surface. Furthermore, *E. rufidulum* lacks black scales on the abaxial surface of the costa, which are present in *E. splendens*. Specimens from the Comoro Islands closely resemble and may be conspecific with *E. rufidulum*, but these collections have been referred to *E. tanganjicense* Krajina ex Pic. Serm. (see Pichi Sermolli, 1968: 238), which does not occur in the Mascarenes. *Elaphoglossum kuhnii* Hieron. of tropical Africa (absent in the Masacarenes) is also closely related. This complex, which occurs from tropical America to Macaronesia, tropical Africa, the Malagasy region, and Hawai'i, is in need of critical study.

Specimens examined. RÉUNION. Volcan, Massif de la Fournaise, l'Enclos Fouqué, près du Pas de Bellecombe, *Cadet 1535* (P, REU); Pas de Bellecombe, bord du sentier descendant dans l'Enclos, *Rouhan & Grangaud 224* (P), *Des Abbayes 2950* (P).

17. Elaphoglossum ×setaceum Lorence [*Elaphoglossum hybridum* (Bory) Brack. × *E. lanatum* (Bojer ex Baker) Lorence], Fern Gaz. 12: 348, fig. 5. 1984. TYPE: Mauritius. Tamarind Falls Reservoir, 1973, *D. H. Lorence s.n.* (holotype, MAU 15823b!).

Plant with fronds caespitose, borne in 3 ranks; rhizome very short-creeping, 3 mm diam., unbranched, densely paleaceous; scales 3–4 × 0.5 mm, lanceolate to narrowly ovate, light castaneous, base cordate, apex filiform, margins bearing short teeth each terminated by a globose gland, cells rectangular-fusiform. Phyllopodia 2–4 mm long,

dark brown, paleaceous; sterile fronds 8–14 cm; stipe 3–3.5 cm, 0.5–0.7 mm diam., yellowish brown, canaliculate, bearing numerous simple capitate hairs and abundant, brown, squarrose, subulate scales 1.5–2.5 × 0.2 mm, base cochleariform, apex filiform, margins involute, bearing several long cilia and short glandular teeth or cilia; blade narrowly elliptic to narrowly ovate, (5–)9–10.5 × (1–) 1.5–2 cm, base narrowly cuneate, decurrent as low ridges along stipe, apex acuminate, chartaceous, costa prominulous on both surfaces, yellow brown, both surfaces bearing spreading subulate scales as in stipe, margins slightly revolute, rounded, ciliate with fringe of pale brown, spreading, bristle-like scales 2–3 × 0.2–0.3 mm, base cochleariform, apex filiform, margins involute basally and bearing several long, spreading glandular-tipped cilia and sparse short hair teeth, veins distinct, bifurcate, apically free, tips thickened, both surfaces of blade villous with bristle-like scales intermixed with smaller flat, deltate scales, each with a single pair of long, spreading basal cilia and scattered simple hairs. Fertile frond and spores unknown.

Distribution and habitat. Mauritius, known only from the type locality at 500 m in secondary forest. A single sterile individual of this nothospecies was found growing in a population of *E. lanatum* on a shady stream bank with *E. hybridum* var. *hybridum* growing on a tree directly overhead (Lorence, 1984).

Discussion. *Elaphoglossum* ×*setaceum* possesses morphological characters almost exactly intermediate between those of the putative parents, notably shape of the blade and scale characters. Furthermore, *E.* ×*setaceum* presents a rhizome bearing three ranks of fronds, whereas *E. lanatum* is a two-ranked species and *E. hybridum* var. *hybridum* has four ranks (Lorence, 1984).

18. Elaphoglossum sieberi (Hook. & Grev.) T. Moore, Index Fil.: 14. 1857. *Acrostichum sieberi* Hook. & Grev., Icon. Filic. tab. 237. 1831. *Olfersia sieberi* (Hook. & Grev.) C. Presl, Tent. Pterid. 235. 1836. TYPE: Mauritius. *W. Bojer s.n.* (lectotype, designated by Lorence (1976: 204), K! [Hb. Hook., pro parte, left-hand specimen only]). Figure 1E.

Fronds densely caespitose, borne in 2 ranks; rhizome very short-creeping, 7–10 mm diam., unbranched, densely paleaceous; scales 8–20 × 0.5–1 mm, narrowly linear-ovate, dull brown to black, base enlarged, cordate to auriculate, distally filiform and often sinuate, the margins fringed basally with short, glandular projections, medially and apically entire or rarely with short, glandular projections, the cells narrowly rectangular-fusiform with thick, dark walls (Fig. 5F). Phyllopodia 6–15 mm long, swollen, articulated, dark brown to black, paleaceous; sterile fronds 20–45(–65) cm; stipe 5–15(–25) cm × 2–4 mm, stramineous, terete, bearing scattered brown to black, appressed-persistent scales 5–10 × 0.25–0.5 mm, base stellate with glandular cilia, apex filiform; blade narrowly ovate to elliptic or linear-elliptic, 15–30(–42) × 4–6(–9) cm, base narrowly to broadly cuneate, sometimes attenuate and decurrent, apex acute to obtuse or rounded, subcoriaceous to coriaceous, costa prominulous, rounded abaxially, flattened to canaliculate adaxially, margins revolute, veins indistinct, bifurcate 1 to 2 times, uniting apically into an intramarginal commissure, adaxial surface of blade glabrate, abaxial surface of blade with scattered, appressed brown scales 0.5 mm diam., stellate with bulbous-tipped cilia (Fig. 5G). Fertile frond 16–30(–45) cm long; stipe as in sterile frond; blade narrowly elliptic to linear-elliptic, 6–20(–36) × 1.2–2.6(–4) cm, apex acute to obtuse, base cuneate to attenuate, slightly decurrent, veins visible adaxially. Spores 35–38 × 23–26 μm (excluding perispore), the perispore cristate, crisped, the crests 4–10 μm high with erose-dentate margins.

Distribution and habitat. Mauritius, endemic. One of the most commonly encountered members of the genus on Mauritius. *Elaphoglossum sieberi* grows as an epiphyte to 10–12 m above ground or casually terrestrial, in moist and wet forests and ericoid shrublands, at 200 to 900 m.

Discussion. *Elaphoglossum sieberi* resembles *E. macropodium* by the shape, texture, and size of the fronds, but can be distinguished from *E. macropodium* and all others in the Mascarenes by a thinner rhizome (7–10 mm diam.) densely clothed with long (8–20 mm), narrowly linear-ovate, dull brown to black scales.

Selected specimens examined. MAURITIUS. Alexandra Falls, *Rouhan et al. 169* (MAU, NY, P, PTBG); Bassin Blanc, 1966, *Edgerley s.n. in MAU 12464* (MAU, P); Curepipe, Kanaka, 1906, *Bijoux s.n.* (MAU); Curepipe, *Vaughan in MAU 2566* (MAU); Deux Mamelles Mtn., *Lorence in MAU 15016* (MAU); Ferney, mtn. ridge, *Lorence 773 in MAU 16314* (MAU); Le Pouce Mtn., Aug. 1849, *Boivin s.n.* (P); Les Mares, *Rouchecouste & Orian s.n.* (MAU [2]); Macabé, *Lorence in MAU 14584* (MAU); Macabé–Brise Fer rd., *Lorence in MAU 14586* (MAU); Mt. Deux Mamelles, *Lorence in MAU 15016* (MAU, P); Mt. Lagrave, E flank, *Lorence 779 in MAU 16318* (MAU), *Lorence 782 in MAU 16313* (MAU); Pétrin Nat. Reserve, *Lorence in MO M129* (MO, P); Pétrin–Les Mares rd., *Vaughan in MAU 12624* (MAU); Piton Combo, *Lorence 890* (MO); Piton du Milieu, *Lorence 10.2 in MAU 15814* (MAU, REU); Piton Grand Bassin, *Lorence 1074* (MO); Piton

Grand Fond, *Lorence 301* (MO); Plaine Champagne nr. Cascade 500 Pieds, *Lorence s.n.* (MO); Plaine Champagne–Chamarel rd., headwaters of Rivière Saint Denis, *Julien in MAU 14585* (MAU); Plaine Champagne–Bel Ombre rd., *Lorence 9.1* (MO); Plaine Champagne near Plaine Paul, *Lorence 2.2* (MO); Plaine Paul near path to Mt. Cocotte, *Vaughan in MAU 12593* (MAU).

19. Elaphoglossum spatulatum (Bory) T. Moore, Index Fil.: 14. 1857. *Acrostichum spatulatum* Bory, Voy. Iles Afrique 1: 363, tab 20, fig. 1. 1804. TYPE: Bourbon [Réunion]. Rivière St. Denis, "an X" [1801–1802], *J. B. G. G. M. Bory de St. Vincent s.n.* [Hb. Bory 27,34] (holotype, P!). Figure 4C, D.

Fronds caespitose, borne in 3(to 4) ranks; rhizome very short-creeping, 1.5–2 mm diam., short and unbranched, densely paleaceous; scales 3–4 × 0.3–0.4 mm, narrowly ovate, membranaceous, reddish brown, base cordate to auriculate, apex narrowly acuminate, filiform, margins entire, cells fusiform. Phyllopodia absent; sterile fronds 3–7(–9) cm; stipe 2–4(–6) cm, 0.5 mm diam., stramineous, slightly canaliculate, densely paleaceous with spreading, narrow, reddish brown, subulate scales 2–3 × 0.3–0.4 mm, base cordate, the lobes involute, apex long-acuminate, margins with scattered short teeth basally, distally entire; blade narrowly obovate-spatulate to narrowly elliptic, 1.5–4(–5.5) × 0.5–0.8(–1.2) cm, base narrowly cuneate and decurrent, apex obtuse or rarely acute, thickly chartaceous, costa prominulous and rounded on both surfaces, margins thin, cartilaginous, revolute, veins bifurcate, apically free, tips thickened and dark, both surfaces of blade and margins with scattered slender, subulate scales like those on stipe but smaller, mixed with simple capitate trichomes. Fertile frond slightly longer than sterile frond, 5–8(–10) cm long; stipe slender, often longer than sterile stipe; blade 1–2.3 × 0.7–1 cm, ovate, elliptic, or obovate, conduplicate before maturity, base cuneate, shortly decurrent, apex obtuse, often emarginate, adaxial surface paleaceous as in fertile frond, margins thin, cartilaginous. Spores 30–35 × 20–25 μm (excluding perispore), surface cristate, crests 3–5 μm high with entire, sinuate margins.

Distribution and habitat. Réunion, Mauritius; also known from Madagascar, tropical Africa, extratropical southern Africa, and Sri Lanka (Sledge, 1967). This diminutive species is common on Réunion where it grows exclusively on mossy boulders and rocks in the beds of rivers and streams from 900 to 1400 m. On Mauritius *E. spatulatum* is known only from two collections made over a century ago; it may be extirpated.

Discussion. *Elaphoglossum spatulatum* can be easily distinguished from all other *Elaphoglossum* in the Mascarenes by the small fronds 3–7(–9) cm long bearing subulate scales and the fertile fronds conduplicate before maturity. Furthermore, *E. spatulatum* is unique in growing exclusively on boulders in the beds of rivers.

Elaphoglossum spatulatum greatly resembles *E. piloselloides* (C. Presl) T. Moore, a tropical American species (Moran & Smith, 2001), but *E. spatulatum* differs by having the scales of the fertile fronds orange-tan rather than black (Mickel, 2002). The close relationship between both species is strongly supported by phylogenetic analyses based on molecular data, since *E. spatulatum* and *E. piloselloides* appear more related to each other than to any other species in the genus (Rouhan et al., 2004). Thus, *E. spatulatum* may possibly be conspecific with *E. piloselloides* (in which case *E. spatulatum* would have priority).

Selected specimens examined. MAURITIUS. Woods of Grand Port and Savanne, [probably Bijoux], *s.d., s.n, ex Hb. Pamplemousses s.n.* (MAU). RÉUNION. Basse Vallée, Ravine Pérote, *Rouhan 235* (NY, P, PTBG); Bébour, *Rouhan & Grangaud 246* (NY, P, PTBG); Brûlé, 1891, *Bedier 51* (P); Hautes de Ste. Marie, *Coode & Cadet 5007* (K, MAU); Montée de la Plaine des Affouches, *Bosser 20460* (P); Montée de la Plaine des Palmistes, *Bosser 9561* (P); Morne de Patates Durand, *Lorence FR6 in MAU 15618* (MAU); Rivière des Marsouins, *M. G. De L'Isle 82* (P); Takamaka, *Guého in MAU 15363* (MAU).

20. Elaphoglossum splendens (Bory ex Willd.) Brack., U.S. Expl. Exped., Filic. 16: 68 1854. *Acrostichum splendens* Bory ex Willd., Sp. Pl. ed. 4, 5: 104. 1810. TYPE: Bourbon [Réunion]. An X [1801–1802], *J. B. G. G. M. Bory de St. Vincent s.n.* [Hb. Bory 27,25] (holotype, B-W 19515, B-W microfiche MO!; isotype, P!). Figure 3A.

Fronds densely caespitose, borne in 4 ranks; rhizome short-creeping, 3–4 mm diam., unbranched, densely paleaceous; scales 2.5–3.5 × 0.6–1 mm, narrowly ovate, castaneous or dark brown, shiny, stiff, base cordate, apex acute, margins bearing short hair teeth (Fig. 6E). Phyllopodia 1–1.5 cm long, slightly swollen, dull brown, densely paleaceous as in rhizome; sterile fronds 25–40(–53) cm; stipe 4–16(–30) cm, 1.5–2 mm diam., pale orange-brown, canaliculate, densely paleaceous, the scales spreading, dark reddish brown, ovate to linear-oblong, 3–5 × 0.5–1.5 mm, base truncate to cordate, apex acute, often black, margins bearing many dark brown to black stiff hair teeth, cells shortly fusiform to irregularly oblong, with thick walls; blade linear-ovate to linear-elliptic, often falcate, 16–24(–33) ×

1.5–2.5(–3.6) cm, base narrowly cuneate to attenuate, apex acute, acuminate or sometimes caudate, chartaceous to subcoriaceous, costa prominulous on both surfaces, adaxially flattened to slightly canaliculate, abaxially rounded, margins rounded, sometimes weakly revolute, fringed with spreading scales, veins bifurcate, apically free, both surfaces of blade covered with a dense, persistent layer of imbricated reddish brown scales aging grayish adaxially, those on abaxial surface of costa usually dark brown to blackish, scales ovate to narrowly ovate, (0.3–)1.5–2.5 × 0.2–0.5 mm, base cordate, apex acute, margins fringed with long, erect-spreading hair teeth (Fig. 6F). Fertile frond as long as sterile frond; stipe 1 to 1.5 times as long as sterile stipe; blade 14–18(–34) × 1.2–1.4(–1.9) cm, linear to linear-elliptic, base cuneate, truncate or cordate, apex acute to obtuse, scales of adaxial surface and abaxial surface of costa as in sterile frond. Spores 38–42 × 25–28 μm (excluding perispore), perispore weakly cristate, crests 2.5–4 μm high, margins entire to sinuate.

Distribution and habitat. Réunion and Mauritius. *Elaphoglossum splendens* is common on Réunion, where it occurs as an epiphyte in the shade of wet forests and cloud forests at 1000 to 2350 m, or occasionally on mossy boulders in ericoid vegetation. It is extremely rare or perhaps extirpated on Mauritius, where it is known only from two collections made in the early 1900s.

Discussion. *Elaphoglossum splendens* resembles *E. rufidulum* in general appearance and by its rhizome and frond scales with stiff hair teeth, but *E. splendens* occurs at lower elevations, and its sterile fronds are more densely paleaceous, with the imbricated scales completely obscuring the frond surface. Furthermore, *E. splendens* has black scales on the abaxial surface of the costa, which are absent in *E. splendens*.

The following misapplied name found in the early Mascarene literature should refer to *E. splendens*: *Acrostichum squamosum* sensu Baker, Fl. Mauritius 512. 1877, sensu Cordem., Fl. Réunion, part 1: 85. 1891, Fl. Réunion 96. 1895, non *Acrostichum squamosum* Sw., J. Bot. (Schrader) 1800(2): 11. 1801.

Selected specimens examined. MAURITIUS. Grand Bassin, Pétrin, *Bijoux 76* (MAU, P); *s.d., s.n., ex Hb. Pamplemousses in MAU 17656* (MAU). RÉUNION. Bébour, *Rouhan & Grangaud 247* (NY, P, PTBG); Bébour, path to Bassin des Hirondelles, *Guého in MAU 15366* (MAU); Cilaos, sentier de la Mare à Joseph au coteau Kerveguen, *Badré 937* (P [2]); Cilaos, sentier GR R1 entre "Le Bloc" et le gîte de la Caverne Dufour, *Rouhan 213* (NY, P, PTBG), *Rouhan 218* (NY, P); Cirque de Salazie, N of Piton Marmite, *Lorence et al. 7544* (MO, PTBG); Cirque de Salazie, *Rouhan et al. 225* (P, PTBG); Col de Bellevue, Grande Montée de la Plaine des Cafres, *Lorence 2463* (MO); Dimitile, *Rouhan & Grangaud 203* (NY, P, PTBG); Grand Matarum, *Lorence in MAU 15631* (MAU), *Staub in MAU 13012* (MAU); Hauts de Saint-Paul, 2 June 1882, *s.d. 74* (P); L'îlet Alcide, *Rouhan et al. 243* (P); Montée de la Plaine des Palmistes, *Bosser 9529* (P [pro parte, left-hand specimen]); Piton des Neiges, near le Gite, *Lorence in MAU 15650 A-C* (MAU); Plaine des Chicots, *Bory de St. Vincent s.n.* (P); Plaine des Fougères, *Boivin 799* (P); St. Philippe, *Schlieben 10934 1* (MAU 12441); Tévelave near Les Avirons, *Schlieben 10849* (MO); s. loc., *Commerson s.n.* (P-JU 1002).

21. Elaphoglossum stipitatum (Bory ex Fée) T. Moore, Index Fil.: 15. 1857. *Acrostichum stipitatum* Bory ex Fée, Mém. Foug., 2: 38, tab. 4(3). 1844 [1845]. TYPE: Bourbon [Réunion]. Salazie, *s.d., s.n.* [Hb. Bory 27,12] (holotype, P!). Figure 3D.

Fronds spaced 0.5–1.5 cm, borne in 2 ranks; rhizome long-creeping, 1.5–2 mm diam., occasionally branched, densely paleaceous; scales 3–5 × 0.4–0.6 mm, narrowly ovate to linear-ovate, dark reddish brown to blackish, paler basally, base cordate to sagittate, apex narrowly acuminate, sinuate, filiform, margins bearing short, often paired hair teeth, cells fusiform, in rows (Fig. 6G). Phyllopodia 3–6 mm long, slightly swollen, dark brown; sterile fronds 8–22(–44) cm; stipe 3–16(–25) cm, 0.5–1 mm diam., flexuous, stramineous to yellowish brown, bearing numerous, spreading, rusty, narrowly ovate scales 2–3 × 0.3–0.8 mm, base cordate to auriculate, apex long-acute, slender, margins with short hair teeth, brown resinous punctations also present; blade oblong- to linear-ovate or oblong- to linear-elliptic, 4.5–8(–19) × 0.9–1.5(–2) cm, base cuneate to narrowly cuneate, shortly decurrent, apex acute to obtuse, subcoriaceous to coriaceous, costa prominulous and rounded abaxially, flattened to shallowly canaliculate adaxially, both surfaces of blade bearing spreading scales as in stipe, margins thin, revolute, veins distinct, unbranched or 1 to 2 times bifurcate, apically free, adaxial surface thinly covered with rusty to gray or white, narrowly ovate scales 1–2 × 0.2–0.3 mm long, base cordate to sagittate, apex slender, margins and basal lobes bearing long, paired hair teeth, cells rectangular to fusiform (Fig. 6H), abaxial surface glabrous except costa bearing scattered scales like those on adaxial surface of blade, both surfaces of blade bearing short capitate trichomes and brown resinous punctations. Fertile frond about equaling sterile frond; stipe slender, 1.5 to 2.5 times longer than sterile stipe; blade 5–7(–8.5) × 1–1.2(–1.4) cm, shape and scales of adaxial surface as in sterile frond. Spores 38–40 × 25–30 μm (excluding perispore),

perispore cristate, crests 3–6 μm high, margins erose-dentate.

Distribution and habitat. *Elaphoglossum stipitatum* is endemic to Réunion, where it occurs on rocks or terrestrially in mats of bryophytes at 2000 to 2500 m, or in ericoid *Philippia* Klotzsch shrublands.

Discussion. *Elaphoglossum stipitatum* can be distinguished by its sterile fronds with an adaxially scaly, abaxially glabrous blade surface bearing short capitate trichomes, and brown resinous punctations. Furthermore, it is not epiphytic but occurs at high elevations on rocks or terrestrially.

Elaphoglossum stipitatum is very closely allied to or perhaps conspecific with *E. subcinnamomeum* (H. Christ) Hieron. from Kenya, Tanzania, and Cameroon. Both species grow at high elevations and exhibit short capitate trichomes in addition to similar scale characters. Nevertheless, we refrain from placing *E. subcinnamomeum* in synonymy until more specimens of this species have been collected and examined.

Selected specimens examined. RÉUNION. Cilaos, GR R1 entre "Le Bloc" et le gîte de la Caverne Dufour, *Rouhan 212* (NY, P, PTBG); Cratère Commerson, *M. G. De L'Isle 396 bis* (P [2]); Piton des Neiges, *Lorence 407* (MO); Plaine des Salazes, *Cadet 2048* (P); Salazie, *s.n.* [Hb. Bory 27,12] (P); Sommet du Grand Bénard, 16 Feb. 1847, *Boivin 1847–1852* (P); Volcan, Pas de Bellecombe, *Rouhan & Grangaud 221* (NY, P, PTBG).

22. Elaphoglossum tomentosum (Bory ex Willd.) H. Christ, Farnkr. Erde 37. 1897. *Acrostichum tomentosum* Bory ex Willd., Sp. Pl. ed. 4, 5: 101. 1810. TYPE: "B. Ile de France" [Mauritius]. *J. B. G. G. M. Bory de St. Vincent s.n.* [Hb. Bory 27,26] (lectotype, designated by Rouhan & Lorence (2003: 840), P!). Figure 2E.

Fronds caespitose, borne in 2 ranks; rhizome short-creeping, 4 mm diam., occasionally branched, moderately paleaceous; scales 1.5–3 × 0.25–0.5 mm, triangular to unguiculate, dull dark brown, appressed, persistent, base truncate to cordate, apex acuminate, margins entire, scarious to erose, cells opaque. Phyllopodia 8–10 mm long, slightly swollen, brown to dark brown, bearing scales as in rhizome; sterile fronds 25–40(–50) cm; stipe 4–8(–11) cm, 1.2–2 mm diam., pale yellowish orange, canaliculate, narrowly winged distally, when young bearing numerous, dull brown, opaque elliptic to unguiculate scales 1.5–2.5 mm long, 0.4–0.6 mm wide, margins fimbriate, cells fusiform to irregularly polygonal-rounded, thick-walled; blade linear-oblong, 20–40(–44) × 2–3(–4.6) cm, base cuneate to narrowly cuneate to attenuate, apex acute to long-acuminate, subcoriaceous, costa prominulous and rounded abaxially, shallowly canaliculate adaxially, yellowish orange, margins rounded, slightly revolute, veins unbranched or bifurcate, tips apically uniting into an intramarginal commissure, both surfaces of young blade covered by a thin but dense layer of closely appressed, contiguous ovate to scutelliform, peltate scales 0.5–1 mm diam., pale brown or gray with darker centers, margins fimbriate, central cells square, marginal cells elongate (Fig. 5H), adaxial blade surface glabrescent. Fertile frond 20–28(–38) cm long; stipe slender, as long as or slightly exceeding sterile stipe; blade 13–19(–23) × 0.9–1.3(–2.3) cm, narrowly elliptic to linear-elliptic, base cuneate to attenuate, apex acute, adaxial surface bearing a dense layer of contiguous scales as in sterile frond. Spores 35–38 × 23–25 μm (excluding perispore), perispore cristate, 5–7.5 μm high with finely erose-dentate margins.

Distribution and habitat. Mauritius, endemic. Wet forests from 300 to 900 m, growing epiphytically to 10 m above the ground, and occasionally on boulders or terrestrially. Although three old collections are said to be from Bourbon [Réunion], no recent collections are known from that island.

Discussion. *Elaphoglossum tomentosum* resembles *E. heterolepis* by the blade covered by a thin continuous layer of appressed scales, but differs by veins that unite apically into an intramarginal commissure, by its single type of laminar scales that form a thin layer over the blade, and by the dull brown, monochrome rhizome and stipe scales. On Mauritius *E. tomentosum* occasionally hybridizes with *E. heterolepis* producing the nothospecies *E.* ×*heterophlebium*. It also hybridizes with the endemic *E. lanatum* producing *E.* ×*adulterinum* (Lorence, 1984).

The following misapplied name is very common in the literature for the Mascarene area: *Elaphoglossum* (or *Acrostichum*) *obductum* sensu auct. (see discussion under *E. lancifolium*).

Selected specimens examined. MAURITIUS. Alexandra Falls, *Rouhan et al. 178* (MAU, NY, P, PTBG); Bel Ombre nat. reserve, *Lorence in MAU 14605* (MAU); Brise Fer, *Lorence 17.1* (MO); Crown Land Declerc, *Lorence 297* (MO); Gorges de la Rivière Noire, Crown Land Le Bouton, *Lorence 1092* (MO, P); Le Pouce Mt., *Julien in MAU 15180* (MAU); bois de la partie supérieure, Aug. 1849, *Boivin s.n.* (P); Macabé forest, *Lorence 1303* (MO); Macabé, sentier menant à la Mare aux Joncs, *Rouhan et al. 180* (MAU, NY, P, PTBG); Macabé-Brise Fer rd., *Lorence in MAU 14601* (MAU); Mare Longue, *Vaughan in MAU 10084* (MAU); Mt. Lagrave, E flank, *Lorence 793 in MAU 18780* (MAU); Pétrin–Macabé rd., *Lorence in MAU 14587* (MAU); Pétrin Nat. Reserve, *Lorence 13.5 in MAU 15817*

(K, MAU, MO, P, REU); Plaine Champagne, *Lorence in MAU 15011* (K, MAU, P, REU); valley of Cascade 500 Pieds, *Lorence 1166* (K, MO); valley above Cascade 500 Pieds, *Lorence et al. 6990* (MAU, PTBG). RÉUNION. [Probably in error], *s.l.*, Habitat in insula Borboniae [Réunion], *Bory de St. Vincent s.n.* [legit. Flügge, in sched.], (B-W 19508), *Sieber s.n.* ex Hb. Bernardi (MO), *s.n., ex Hb. Pamplemousses s.n.* (MAU).

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APPENDIX 1. List of species and varieties.

1. *Elaphoglossum acrostichoides* (Hook. & Grev.) Schelpe
2. *Elaphoglossum* ×*adulterinum* Lorence
3. *Elaphoglossum angulatum* (Blume) T. Moore
4. *Elaphoglossum aubertii* (Desv.) T. Moore
5. *Elaphoglossum* ×*cadetii* Lorence
6. *Elaphoglossum coursii* Tardieu
7. *Elaphoglossum heterolepis* (Fée) T. Moore
8. *Elaphoglossum* ×*heterophlebium* Lorence
9. *Elaphoglossum hybridum* (Bory) Brack.

9a. *Elaphoglossum hybridum* (Bory) Brack. var. *hybridum*

9b. *Elaphoglossum hybridum* var. *vulcani* (Lepervanche ex Fée) H. Christ

10. *Elaphoglossum lanatum* (Bojer ex Baker) Lorence
11. *Elaphoglossum lancifolium* (Desv.) C. V. Morton
12. *Elaphoglossum lepervanchei* (Bory ex Fée) T. Moore
13. *Elaphoglossum macropodium* (Fée) T. Moore
14. *Elaphoglossum* ×*revaughanii* Lorence
15. *Elaphoglossum richardii* (Bory ex Fée) H. Christ
16. *Elaphoglossum rufidulum* (Willd. ex Kuhn) C. Chr.
17. *Elaphoglossum* ×*setaceum* Lorence
18. *Elaphoglossum sieberi* (Hook. & Grev.) T. Moore
19. *Elaphoglossum spatulatum* (Bory) T. Moore
20. *Elaphoglossum splendens* (Bory ex Willd.) Brack.
21. *Elaphoglossum stipitatum* (Bory ex Fée) T. Moore
22. *Elaphoglossum tomentosum* (Bory ex Willd.) H. Christ

APPENDIX 2. Index to exsiccatae.

The numbers in parentheses refer to the corresponding species and varieties in the text and in Appendix 1. Specimens are listed in alphabetic order by first collector. Collection numbers in **boldface type** indicate type specimens.

Badré 866 (1), 896 (7), 937 (20), 960 (9b), 985 (7), 1004 (4), 1005 (9a); Bédier 51 (19), 52 (12), 53 (7), 54 (13), 56 (15), 57 (15); Bijoux 69 in MAU 2570 (11), 73 (13); Boivin [1847–1852] (21), 799 (20), 800 (7), 801 (1), 802 (13); Bosser 9529 (20), 9544 (4), 9559 (13), 9561 (19), 11857 (9a), 20432 (13), 20460 (19), 20624 (11), 21012 (6), 21503 (4), 21759 (4), 22485 (13).

Cadet 123 (4), 317 (13), 319 bis (11), 504 (3), 805 (1), 879 (15), 880 (7), 1535 (16), 1556 (3), 1556 (9a), 1702 (7), 1749 (1), 1778 (3), 1929A (1), 1930 (3), 1930 bis (7), 2048 (21), **2063 (5),** 3718 (11), 3766 (12), 3790 (7), 3884 (15), 4017 (12), 4028 (1), 4122 (1), 4126 (6), 4127 (11), 4130 (12); Coode 5007 (19).

De L'Isle 82 (19), 396 bis (21); Des Abbayes 2950 (16); Du Petit-Thouars **s.n. [1801] (11), s.n. [1808] (4).**

Edgerley s.n. in MAU 12464 (18).

Guého in MAU 11498 (9a), in MAU 15303 (11), in MAU 15362 (11), in MAU 15363 (19), in MAU 15366 (20).

Humbert **24918** (6).

Julien in MAU 13318 (12), in MAU 14585 (18), in MAU 14594 (11), in MAU 14595 (9a), in MAU 15180 (22), in MAU 16494 (9a).

Lépervanche-Mézières **14** (3); Lorence 2.2 (18), 2.3 in MAU 15831 (12), 2.11 (7), 3.1 in MAU (12), FR6 in MAU 15618 (19), 7.3 in MAU 15813 (11), 8.5 (11), 8.6 in MAU 15531 (14), 9.1 (18), 10.2 in MAU 15814 (18), 10.3 (11), 11.1 (14), 12.1 in MAU 15822 (12), 13.5 in MAU 15817 (22), 14.1 in MAU 15811 (12), **14.2 in MAU 15821** (8), **14.3 in MAU 15818** (14), 16.2 in MAU 15819 (8), 17.1 (22), 17.2 in MAU 15830 (10), 18.3 in MAU 15812 (12), 21.1 in MAU 16280 (10), M129 (18), 300 (7), 301 (18), 318 (11), 327 (12), 407 (21), 408 (3), 506 (11), 773 (18), 779 in MAU 16318 (18), 782 in MAU 16313 (18), 783 in MAU 16317 (7), 792 in MAU 16315 (11), 793 in MAU 18780 (22), 828 in MAU 16319 (12), **847** (2), 890 (18), 996 in MAU 16518 (8), 1074 (18), 1078 (7), 1092 (22), 1166 (22), 1173 (10), 1176 (14), 1303 (22), 1374 (11), 1102 (7), 1406 (10), 1420 in MAU 17544 (7), 1479 (11), 1197 (14), 1544 (8), 1608 (9a), 1609 (2), 1610 (2), 1626 (12), 2463 (20), 2496 (9b), 2520 (1), 6944 (9a), 6990 (22), 7017 (11), 7544 (20), 7561 (6), in MAU 14584 (18), in MAU 14586 (18), in MAU 14587 (22), in MAU 14588 (12), in MAU 14589 (12), in MAU 14599 (7), in MAU 14601 (22), in MAU 14605 (22), in MAU 14609 (7), in MAU 14610 (12), in MAU 14640 (12), in MAU 14880 (12), in MAU 15010 (12), in MAU 15011 (22), in MAU 15016 (18), in MAU 15024 (9a), in MAU 15099 (8), in MAU 15242 (12), in MAU 15243 (10), in MAU 15533 (10), in MAU 15612 (3), in MAU 15614 (1), in MAU 15615 (3), in MAU 15619 (7), in MAU 15620 (13), in MAU 15621 (1), in MAU 15622 (9a), in MAU 15623 (1), in MAU 15625 (9b), in MAU 15625a (9a), in MAU 15626 (9a), in MAU 15628 (11), in MAU 15629 (4), in MAU 15630 (15), in MAU 15631 (20), in MAU 15637 (1), in MAU 15638 (13), in MAU 15640 (3), in MAU 15642 (12), in MAU 15644 (15), in MAU 15645 (7), in MAU 15647 (15), in MAU 15648 (1), in MAU 15650 A-C (20), in MAU 15816 (7), in MAU 15823 (10), in MAU 15823a (9a), **in MAU 15823b** (17), in MAU 16018 (7), in MAU 16019 (7), in MAU 16307 (2), in MAU 18785 (7).

Richard **10** (15); Rouhan 169 (18), 175 (12), 177 (7), 178 (22), 179 (7), 180 (22), 181 (11), 187 (11), 188 (12), 190 (14), 192 (10), 193 (11), 194 (10), 195 (9a), 197 (11), 198 (9a), 199 (6), 201 (11), 202 (7), 203 (20), 204 (1), 205 (15), 206 (4), 207 (13), 208 (12), 209 (13), 210 (11), 211 (7), 212 (21), 213 (20), 214 (9b), 215 (1), 216 (3), 217 (9a), 218 (20), 219 (9b), 220 (3), 221 (21), 222 (9b), 224 (16), 225 (20), 226 (4), 227 (12), 228 (9a), 229 (1), 231 (15), 232 (13), 233 (3), 234 (15), 235 (19), 236 (11), 239 (9a), 241 (4), 242 (1), 243 (20), 244 (15), 246 (19), 247 (20), 248 (12), 249 (1), 250 (9a).

Schlieben 10849 (20), 10928 in MAU 12416 (11), 10934 (7), 10934 1 (20); Sieber Flora Mixta **281** (7); Staub in MAU 11348 (9a), in MAU 13012 (20).

Vaughan in MAU 2566 (18), in MAU 10084 (22), in MAU 12544 (11), in MAU 12551 (12), in MAU 12593 (18), in MAU 12624 (18).

Wiehe 1721 (3).

COMPARATIVE WOOD ANATOMY OF THE BLUEBERRY TRIBE (VACCINIEAE, ERICACEAE S.L.)[1]

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Abstract

Wood samples of 111 Vaccinieae specimens (Vaccinioideae, Ericaceae s.l.) representing 98 species and 26 genera are investigated with light microscopy and scanning electron microscopy. The wood structure of Vaccinieae delivers taxonomically important characters that can be used to define some subclades within the tribe. The wood of the large polyphyletic genus *Vaccinium* strongly resembles non-vaccinioid members of the family, which are characterized by bordered vessel-ray pits and relatively narrow (2- to 4-seriate) and low multiseriate rays (often less than 1000 μm) with exclusively or mainly procumbent body ray cells. The East Malesian clade, Meso-American/Caribbean clade, and the Andean clade show a combination of wood anatomical features that is lacking in other representatives of the family. These features include scalariform vessel-ray pits with strongly reduced borders, a high portion of upright body ray cells, wide (4- to 14-seriate) and high multiseriate rays (often more than 3000 μm), and prismatic crystals in chambered ray cells (although absent in *Symphysia racemosa*). The presence of secretory ducts in the primary xylem and in the pith tissue may represent a synapomorphy for the Andean clade. Furthermore, the presence of undivided axial parenchyma cells, usually ranging from 500 to 900 μm, seems to be unique in the subfamily.

Key words: blueberries, comparative wood anatomy, Ericaceae, Neotropics, secretory ducts, systematics, Vaccinieae.

The tribe Vaccinieae Rchb. (Ericaceae Juss. s.l.) comprises about 35 genera and more than 1000 species. Most representatives are evergreen shrubs, many occurring as epiphytes and occasionally as lianas. The vast majority of the taxa (about 30 genera and 900 species) are concentrated in the cooler, moist, montane areas of South America between 1500 and 3000 m (Luteyn, 2002). The remaining taxa are concentrated in the montane regions of southeast Asia and Malesia, and a few species are restricted to southeast Africa and Madagascar. *Vaccinium* L., the only genus that occurs in the tropics of the Old and New World, is by far the largest of the tribe (ca. 450 species), but it does not seem to be monophyletic according to molecular data (Kron et al., 2002b).

Hooker (1876) considered the blueberry tribe as a separate family, Vacciniaceae Gray, particularly because of the inferior ovary and the fleshy fruit. Based on the overwhelming similarities between Vacciniaceae and Ericaceae, most authors placed the study group as a tribe within the subfamily Vaccinioideae Arn. of the Ericaceae (Drude, 1897; Stevens, 1971). In the classification of Stevens (1971), the circumscription of Vaccinioideae was greatly enlarged by the inclusion of Arbuteae Meisn., Andromedeae Klotzsch, Cassiopeae P. F. Stevens, and Enkiantheae P. F. Stevens. In the most recent classification of Kron et al. (2002a), based on molecular as well as morphological data, Vaccinieae are sister to Andromedeae s. str. and Gaultherieae Nied., which form together with Lyonieae Kron & Judd and Oxydendreae H. T. Cox the rest of the subfamily Vaccinioideae.

Within the study group, the systematic relationships are far from resolved. Many earlier botanists divided Vacciniaceae into two tribes, namely Vaccinieae and Thibaudieae Benth. & Hook.f., based

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on flower morphology and leaf anatomy (Hooker, 1876; Niedenzu, 1890; Drude, 1897). Nevertheless, the two tribes could not be clearly distinguished from each other because of the variation in the flowers and leaves of some genera. Also the generic boundaries within the study group, traditionally based on flower, fruit, seed, and vegetative characters, caused many problems (Sleumer, 1941; Luteyn, 1991). Nowadays, our knowledge of Vaccinieae has increased significantly, although several genera still remain poorly studied (Stevens, 1985). This can be illustrated, for instance, by molecular sequence data, which show that only few Vaccinieae genera seem to be monophyletic (Kron et al., 2002b). On the other hand, five major evolutionary lines within Vaccinieae could be established, i.e., a large Andean clade with the majority of genera, a Meso-American/Caribbean clade, an East Malesian clade, an *Agapetes* G. Don clade with some Asian *Vaccinium* and *Agapetes* species, and a *Vaccinium* clade with members of *Vaccinium* sections *Bracteata* and *Oarianthe*.

The wood anatomy of the blueberry tribe is only fragmentarily known. Metcalfe and Chalk (1950) commented on the wood anatomy of a few species of *Agapetes*, *Gaylussacia* Kunth, *Macleania* Hook., *Paphia* Seem., *Psammisia* Klotzsch, and *Vaccinium*. Other authors investigated the secondary xylem of several species belonging to only one genus. For instance, Giebel (1983) studied the wood anatomy of *Cavendishia* Lindl., Suzuki and Noshiro (1988) investigated *Agapetes*, and species of *Vaccinium* were treated by, for instance, Flint (1918), Moll and Janssonius (1926), Greguss (1959), Weingartner (1969), Baas (1979), Carlquist (1985, 1988), Odell et al. (1989), Queiroz and Van Der Burgh (1989), Stuzková et al. (2003), and Edwards and Axe (2004).

This work aims to present a detailed wood anatomical overview of the tribe Vaccinieae, including most genera except for *Anthopteropsis* A. C. Sm., *Costera* J. J. Sm., *Didonica* Luteyn & Wilbur, *Gonocalyx* Planch. & Lindl., *Paphia*, *Pellegrinia* Sleumer, *Rusbya* Britton, and *Utleya* Wilbur & Luteyn. Special emphasis is paid to comparison of the wood anatomical variation with recent taxonomic insights based on molecular sequence data in order to reveal possible evolutionary patterns and to look for wood anatomical support in one or more evolutionary lines. The presence of fibers with a living protoplast, as has been discovered previously by several authors in Vaccinioideae (Braun, 1961; Fahn & Leshem, 1962; Giebel, 1983; Lens et al., 2004a), will also be discussed briefly. This manuscript is part of a general wood anatomical survey of Vacciniodeae (Lens et al., 2004a). The ecological wood anatomy of the subfamily is treated elsewhere (Lens et al., 2004b).

Material and Methods

Wood samples of 111 specimens representing 98 species and 26 genera (cf. Index, Table 1) were investigated using light microscopy (LM) and scanning electron microscopy (SEM). For LM observations, transverse and longitudinal sections of about 25 μm were cut using a sledge microtome (Reichert, Vienna, Austria), after softening the wood samples in hot water; a previous warming of the knives is not necessary. Transverse sections of tiny samples were cut using two pieces of polystyrene foam. In order to make tangential and radial longitudinal sections of these thin stems, the sample was mounted with superglue on a rectangular piece of wood that was clamped in the microtome holder. The entire thickness of the wood sample could then be used to produce longitudinal sections. All the sections were bleached with sodium hypochlorite and stained with a mixture of safranin and alcian blue (35:65). The safranin was prepared as a 1% solution in 50% ethanol, while the 1% alcian blue stain was dissolved in pure water. Afterward, the tissues were dehydrated with 50%–75%–96% ethanol and mounted in Euparal. LM observations were carried out using a Dialux 20 light microscope (Leitz, Wetzlar, Germany), and pictures were taken using a DP50-CU digital camera (Olympus, Hamburg, Germany). Preparations for macerations were made using a hot mixture of glacial acetic acid and hydrogen peroxide (Franklin, 1945). For SEM observations, wood samples were softened in hot water. Longitudinal wood sections were made using a razor blade. The sections were bleached with sodium hypochlorite and dehydrated with 50%–75%–96% ethanol. Afterward, the sections were gold-coated with a sputter coater (SPI Supplies, West Chester, Pennsylvania, U.S.A.) and observed using a JEOL JSM-5800 LV scanning electron microscope (JEOL Ltd., Tokyo, Japan), which is situated in the National Botanic Garden of Belgium.

The wood anatomical terminology follows the "IAWA list of microscopic features for hardwood identification" (IAWA Committee, 1989). Because of the difficulties in determining the type of non-perforated tracheary elements, a description is given below.

All types of non-perforated tracheary elements, i.e., tracheids, fiber-tracheids, and libriform fibers, are present in the wood of Ericaceae s.l. (Baas, 1979; Carlquist, 1988; Lens et al., 2003). It may

Table 1. Survey of selected wood anatomical features within Vaccinieae. + = present, − = absent, ± = sometimes present, ? = unknown. [1,2,3,4]Numbers after the names of specimens refer to the order used in the material list. Minimum and maximum values are shown in parentheses. ">" means that the height of the multiseriate ray exceeds the length of the section.

			Vessels								
Species studied	Secretory ducts in pith or primary xylem	Percentage of scalariform perforations	Number of bars	Opposite vessel-ray pitting	Scalariform vessel-ray pitting	Alternate vessel-ray pitting	Simple vessel-ray pitting	Helical thickening throughout vessel elements	Helical thickenings in fibers and/or tracheids	Tangential diameter of vessel lumina (μm)	Vessels per square mm
Agapetes flava	−	10	(1–)4(–6)	±	−	+	−	+	−	(12–)18(–25)	(210–)288(–390)
A. hosseana	−	100	(7–)14(–24)	±	−	+	−	−	−	(10–)18(–30)	(140–)194(–240)
A. mannii	−	100	(6–)9(–11)	±	−	+	−	+	+	(10–)13(–18)	(300–)379(–440)
A. moorei	−	85	(2–)9(–15)	±	−	+	−	−	−	(15–)18(–22)	(120–)145(–200)
A. sikkimensis	−	20	(2–)8(–13)	±	−	+	−	−	−	(19–)25(–30)	(140–)169(–200)
A. variegata	−	20	(7–)10(–12)	±	−	+	−	−	−	(20–)26(–35)	(96–)122(–160)
Anthopterus wardii[1]	?	100	(8–)12(–20)	+	+	−	+	−	−	(15–)20(–30)	(92–)129(–178)
A. wardii[2]	+	90	(1–)7(–15)	+	+	−	+	−	−	(25–)31(–50)	(156–)199(–231)
Cavendishia bracteata	+	70	(1–)5(–9)	−	+	−	+	−	−	(25–)37(–50)	(70–)93(–126)
C. duidae	?	25	(1–)3(–8)	±	+	−	+	−	−	(22–)29(–35)	(140–)166(–192)
C. compacta	?	60	(2–)5(–9)	−	+	−	+	−	−	(30–)39(–50)	(126–)155(–178)
C. lindauiana	+	90	(2–)5(–7)	−	+	−	+	−	−	(25–)39(-50)	(92–)111(–135)
C. pubescens	?	100	(2–)8(–12)	−	+	−	+	−	−	(35–)47(–60)	(36–)44(–58)
C. urophylla	?	70	(3–)5(–8)	−	+	−	+	−	−	(20–)30(–40)	(100–)126(–142)
Ceratostema reginaldii[1]	?	95	(2–)5(–7)	−	+	−	+	−	−	(20–)27(–40)	(54–)91(–122)
C. reginaldii[2]	?	100	(5–)9(–13)	−	+	−	+	±	−	(20–)28(–35)	(32–)51(–95)
Demosthenesia spectabilis	+	100	(2–)5(–7)	+	+	−	+	−	−	(15–)25(–32)	(160–)178(–210)
Dimorphanthera collinsii	?	10	3–4	+	+	−	+	−	−	(110–)163 (–220)	(10-)18(–24)
D. cornuta var. *cornuta*	?	0	0	−	+	−	+	−	−	(60–)103 (–140)	(22–)27(–32)
D. dekockii var. *pubiflora*	?	0	0	−	+	−	+	−	−	(60–)110 (–160)	(16–)24(–32)
D. kempteriana	?	10	9–10	+	+	−	+	−	−	(110–)164 (–205)	(8–)12(–18)
Diogenesia floribunda	−	95	(1–)9(–15)	−	+	−	+	−	−	(20–)30(–40)	(66–)95(–114)
D. tetrandra	+	80	(2–)7(–18)	−	+	−	+	−	−	(20–)27(–40)	(61–)73(–82)
Disterigma. sp. indet.[1]	−	100	(6–)10(–16)	+	+	−	−	+	+	(12–)17(–25)	(240–)362(–415)
D. sp. indet.[2]	?	100	(4–)12(–25)	±	+	−	−	+	+	(12–)17(–20)	(168–)223(–272)
D. alaternoides	−	70	(1–)8(–17)	−	+	−	±	−	−	(25–)35(–45)	(70–)91(–120)
D. cryptocalyx	−	90	(1–)5(–9)	±	+	−	±	−	−	(15–)22(–25)	(120–)152(–180)
Gaylussacia baccata	−	90	(2–)7(–12)	+	+	−	±	+	−	(10–)16(–22)	(215–)307(–370)
G. decipiens var. *decipiens*	−	90	(1–)6(–10)	+	+	−	+	+	−	(15–)20(–30)	(230–)271(–362)

Table 1. Extended.

Vessels	Tracheids	Fibers	Rays			Crystals	
Length of vessel elements (μm)	Length of tracheids (μm)	Length of fiber tracheids (μm)	Multiseriate ray width (number of cells)	Height of uniseriate rays (μm)	Height of multiseriate rays (μm)	Present in rays	Present in axial parenchyma
(370–)472(–580)	(380–)437(–480)	(480–)580(–640)	3–15	(280–)459(–790)	(1300–)2816(–4600)	–	–
(350–)548(–700)	(430–)532(–610)	(620–)724(–910)	1–5	(400–)739(–1300)	(950–)1327(–2150)	–	–
(330–)437(–550)	(350–)481(–570)	(520–)634(–750)	6–9	(600–)850(–1200)	(1100–)1689(–3900)	–	–
(370–)579(–740)	(570–)638(–680)	(700–)783(–970)	6–12	(450–)744(–1000)	1500->8500	±	–
(460–)765(–940)	(670–)805(–900)	(750–)1013(–1180)	5–11	(450–)993(–1600)	>11500	–	–
(530–)704(–840)	(670–)740(–810)	(880–)937(–1070)	6–10	(650–)1766(–3500)	(2400–)3280(–4600)	–	–
(450–)596(–750)	(460–)576(–800)	(600–)829(–1000)	1–5	(600–)936(–1800)	>6000	+	–
(480–)613(–770)	(550–)619(–690)	(680–)823(–930)	1–6	(150–)1069(–2700)	>8000	+	+
(470–)613(–850)	(570–)645(–720)	(690–)941(–1150)	1–5	(250–)577(–1300)	(1000–)2123(–3000)	+	±
(400–)548(–660)	(600–)645(–700)	(670–)833(–970)	1–6	(300–)592(–950)	650->5000	–	–
(270–)657(–880)	(600–753(–950)	(640–)892(–1150)	2–3	(300–)600(–950)	2400->5400	+	±
(280–)590(–820)	(690–)734(–770)	(650–)802(–920)	3–4	(350–)600(–800)	1300->6000	+	+
(450–)619(–820)	(560–)656(–850)	(900–)1060(–1320)	1–5	(550–)744(–850)	(1200–)2036(–2400)	+	–
(390–)598(–750)	(670–)730(–820)	(750–)956(–1140)	3–4	(200–)450(–1000)	(800–)1473(–2200)	+	+
(450–)645(–870)	(580–)693(–1000)	(770–)921(–1100)	3–4	(400–)763(–1400)	(1100–)2605(–5500)	–	
(450–)635(–830)	(480–)530(–670)	(680–)995(–1160)	1–5	(350–)807(–1400)	(900–)1569(–2700)	–	–
(350–)529(–690)	(450–)619(–750)	(560–)695(–820)	1–9	(450–)735(–1200)	(1600–)2267(–3500)	–	–
(550–)754(–1000)	(800–)1016(–1200)	—	3	(300–)605(–1200)	(7000–)8100(–9500)	+	–
(400–)560(–700)	(550–)686(–780)	—	1–6	(200–)406(–550)	(800–)2086(–3600)	+	
(420–)608(–790)	(630–)823(–970)	(820–)990(–1120)	6–11	(300–)492(–950)	(1800–)2843(–5000)	+	–
(700–)930(–1150)	(1100–)1396(–1600)	(800–)990(–1200)	1–7	(300–)804(–1300)	(4000–)6050(–8400)	+	–
(420–)684(–820)	(640–)728(–820)	(720–)889(–1050)	4	(500–)1122(–1750)	>9200	–	
(350–)548(–750)	(500–)608(–700)	(600–)790(–950)	4–5	(350–)780(–1400)	(800–)3920(–6000)	–	–
(250–)364(–550)	(350–)463(–640)	(400–)565(–750)	3	(200–)416(–650)	(500–)643(–1000)	+	–
(300–)330(–450)	(300–)460(–580)	(400–)502(–650)	3	(200–)365(–650)	(400–)693(–1000)	+	
(400–)720(–950)	(560–)752(–900)	(700–)938(–1050)	8–12	(400–)500(–650)	900->5000	±	+
(680–)1006(–1250)	(450–)690(–800)	(1120–)1252(–1880)	3–4	(600–)2357(–5100)	>17500	+	
(280–)393(–500)	(320–)375(–430)	(440–)500(–620)	3–5	(650–)789(–1000)	(800–)1520(–3500)	–	–
(230–)460(–600)	(320–)478(–650)	(560–)688(–960)	4–5	(350–)572(–850)	(2100–)1963(–2700)	–	–

Table 1. Continued.

Species studied	Vessels										
	Secretory ducts in pith or primary xylem	Percentage of scalariform perforations	Number of bars	Opposite vessel-ray pitting	Scalariform vessel-ray pitting	Alternate vessel-ray pitting	Simple vessel-ray pitting	Helical thickening throughout vessel elements	Helical thickenings in fibers and/or tracheids	Tangential diameter of vessel lumina (μm)	Vessels per square mm
Lateropora ovata	+	100	(5–)10(–17)	–	+	–	+	–	–	(15–)23(–30)	(148–)194(–220)
Macleania crassa	?	10	(2–)5(–9)	–	+	–	+	–	–	(35–)49(–60)	(32–)54(–80)
M. ericae	+	85	(2–)5(–9)	–	+	–	+	–	–	(20–)29(–40)	(90–)110(–130)
M. hirtiflora	+	95	(2–)7(–13)	–	+	–	+	–	–	(20–)26(–30)	(83–)108(–148)
M. loeseneriana	?	90	(3–)7(–10)	–	+	–	+	–	–	(20–)33(–50)	(48–)69(–90)
M. pentaptera	?	0	0	–	+	–	+	–	–	(27–)33(–40)	(32–)58(–98)
M. rupestris	?	0	0	–	+	–	+	–	–	(25–)51(–75)	(44–)55(–68)
M. stricta	+	45	(2–)6(–10)	–	+	–	+	–	–	(25–)34(–40)	(91–)105(–123)
Mycerinus chimantensis	–	100	(1–)5(–7)	–	+	–	+	–	–	(20–)25(–35)	(105–)132(–160)
Notopora cardonae	–	15	(3–)6(–11)	–	+	–	+	–	–	(35–)45(–60)	(68–)85(–105)
N. schomburgkii	–	0	0	–	+	–	+	–	–	(30–)46(–65)	(46–)61(–80)
Oreanthes ecuadorensis	+	100	(3–)6(–12)	–	+	–	+	–	–	(20–)26(–30)	(180–)250(–290)
Orthaea fimbriata	+	80	(2–)6(–13)	–	+	–	+	–	–	(20–)31(–40)	(51–)62(–78)
Plutarchia ecuadorensis	–	100	(3–)4(–6)	–	+	–	+	–	–	(15–)20(–35)	(130–)145(–172)
P. rigida	–	95	(2–)4(–6)	–	+	–	+	–	–	(20–)25(–30)	(120–)146(–170)
Polyclita turbinata	+	25	(1–)3(–6)	–	+	–	+	–	–	(25–)28(–40)	(81–)96(–120)
Psammisia sp. indet.	?	0	0	–	+	–	+	–	–	(65–)85 (–120)	(24–)33(–40)
P. ecuadorensis	+	75	(1–)5(–8)	–	+	–	+	–	–	(25–)38(–55)	(53–)74(–90)
P. ferruginea	?	25	(3–)8(–13)	–	+	–	+	–	–	(50–)73 (–120)	(34–)41(–52)
P. graebneriana	+	95	(1–)7(–14)	–	+	–	+	–	–	(15–)26(–35)	(83–)97(–110)
P. guianenis	+	20	(8–)10(–15)	–	+	–	+	–	–	(25–)37(–60)	(60–)72(–90)
P. guianensis	+	85	(1–)8(–13)	±	+	–	+	–	–	(25–)42(–65)	(58–)79(–106)
P. penduliflora	+	100	(3–)4(–9)	–	+	–	+	–	–	(20–)31(–40)	(80–)97(–118)
P. cf. *ulbrichiana*	+	50	(1–)7(–15)	–	+	–	+	–	–	(30–)50(–70)	(32–)42(–50)
Satyria sp. indet.[1]	?	95	(1–)5(–10)	–	+	–	+	–	–	(28–)41(–60)	(34–)52(–66)
S. sp. indet[2]	?	0	0	–	+	–	+	–	–	(65–)93 (–115)	(22–)26(–32)

Table 1. Extended. Continued.

Vessels	Tracheids	Fibers	Rays			Crystals	
Length of vessel elements (μm)	Length of tracheids (μm)	Length of fiber tracheids (μm)	Multiseriate ray width (number of cells)	Height of uniseriate rays (μm)	Height of multiseriate rays (μm)	Present in rays	Present in axial parenchyma
(430–)567(–670)	(520–)577(–620)	(620–)819(–920)	1–6	(550–)950(–1550)	>8000	+	–
(560–)795(–920)	(670–)844 (–1100)	(970–)1117 (–1290)	4–5	(600–)1200 (–1700)	1300->7300	+	+
(460–)653(–750)	(690–)760(–830)	(890–)1012 (–1150)	2–3	(500–)669(–900)	(1100–)2343(–3400)	–	–
(340–)586(–830)	(550–)655(–750)	(850–)974(–1170)	4–5	(550–)821(–1750)	4900->12000	+	+
(400–)617(–800)	(550–)675(–940)	(800–)991(–1200)	3	(300–)446(–1200)	(800–)1645(–3500)	+	
(270–)551(–770)	(440–)520(–600)	(530–)789(–1060)	1–7	(500–)860(–1300)	(1050–)1628(–1950)	+	+
(510–)837 (–1000)	(910–)1109 (–1340)	—	3–5	(350–)1465 (–2700)	3600->10500	+	
(340–)630(–840)	(520–)590(–650)	(830–)928(–1020)	3–4	(1100–)1643 (–2100)	(1800–)4760(–7200)		
(480–)697(–860)	(260–)678(–750)	(720–)864(–1000)	2–3	(550–)1063 (–1900)	(950–)1704(–3200)	+	
(500–)697(–940)	(600–)648(–750)	(580–)862(–1100)	5–7	(550–)983(–1350)	2250->8000	+	
(520–)700(–960)	(550–)725(–850)	(750–)925(–1250)	1–5	(350–)850(–1800)	(600–)2208(–3000)	+	
(420–)649(–979)	(520–)580(–670)	(540–)743(–1040)	1	(450–)700(–1300)	>8500		–
(550–)680(–850)	(540–)745(–880)	(700–)979(–1250)	1–5	(350–)700(–900)	(1100–)3488(–7500)	+	–
(390–)558(–670)	(450–)480(–520)	(600–)716(–850)	7–9	(400–)483(–650)	>2500		–
(400–)556 (–810)	(450–)519(–600)	(550–)749(–860)	1	(650–)1350 (–2000)	>5700		
(320–)561(–780)	(500–)664(–750)	(650–)760(–980)	6–7	(500–)729(–1050)	(1350–)2908(–4950)	+	
(530–)726(–880)	(750–)938 (–1050)	(750–)1095 (–1230)	3–4	(250–)600(–1000)	500->4000	+	+
(520–)694(–870)	(650–)740(–850)	(840–)981(–1260)	3–5	(300–)900(–1500)	1400->8000	+	–
(620–)748(–930)	(730–)871 (–1120)	(870–)1146 (–1380)	4–6	(400–)745(–1100)	5900->10,000	+	–
(340–)579(–770)	(470–)595(–760)	(600–)844(–1060)	4–7	(620–)2478 (–2100)	(5200–)8600 (–10800)	+	–
(700–)900 (–1150)	(650–)939 (–1150)	(1150–)1286 (–1650)	3–4	(250–)696(–1300)	2100->6000	+	–
(580–)696(–880)	(570–)650(–740)	(840–)995(–1170)	6–8	(750–)1710 (–4100)	>13500	+	–
(440–)630(–810)	(580–)639(–680)	(630–)815(–980)	1–5	(1350–)1583 (–2000)	8700->16500	+	–
(500–)668(–800)	(700–)777(–870)	(850–)1005 (–1170)	3–4	(700–)1122 (–1700)	>11000	+	+
(470–)680(–850)	(500–)612(–820)	(720–)967(–1170)	5–6	(500–)740(–1100)	3000->8700	+	–
(450–)684(–870)	(750–)913 (–1100)	(780–)999(–1170)	4–7	(400–)771(–1500)	(1150–)2771(–5300)	+	–

Table 1. Continued.

Species studied	Secretory ducts in pith or primary xylem	Vessels: Percentage of scalariform perforations	Number of bars	Opposite vessel-ray pitting	Scalariform vessel-ray pitting	Alternate vessel-ray pitting	Simple vessel-ray pitting	Helical thickening throughout vessel elements	Helical thickenings in fibers and/or tracheids	Tangential diameter of vessel lumina (μm)	Vessels per square mm
S. sp. indet.[3]	?	0	0	−	+	−	+	−	−	(60–)81 (–100)	(40–)49(–68)
S. sp. indet.[4]	+	40	(1–)5(–9)	−	+	−	+	−	−	(30–)40(–50)	(66–)87(–120)
S. carnosiflora	+	20	(2–)5(–11)	−	+	−	+	−	−	(30–)41(–60)	(59–)79(–110)
S. meiantha	?	15	(2–)4(–6)	−	+	−	+	−	−	(30–)49(–60)	(50–)62(–82)
S. panurensis	?	0	0	+	+	−	+	−	−	(60–)96 (–140)	(24–)28(–30)
S. warszewiczii	+	25	(3–)5(–8)	−	+	−	+	−	−	(20–)35(–40)	(81–)121(–167)
S. warszewiczii	+	70	(2–)6(–11)	−	+	−	+	−	−	(30–)37(–45)	(32–)65(–106)
Semiramisia pulcherrima	+	100	(7–)10(–15)	+	+	−	+	−	−	(14–)21(–27)	(87–)95(–105)
Siphonandra elliptica	?	20	3–4	−	+	−	+	−	−	(25–)36(–50)	(74–)86(–108)
Sphyrospermum sp. indet.	−	95	(2–)9(–20)	−	+	−	+	−	−	(15–)19(–22)	(180–)249(–320)
S. buxifolium	−	100	(8–)10(–12)	+	+	−	+	−	−	(20–)26(–31)	(240–)318(–360)
S. sodiroi	−	100	(8–)11(–14)	−	+	−	+	−	−	(11–)16(–25)	
Symphysia racemosa	−	90	(9–)13(–20)	−	+	−	+	−	−	(20–)33(–40)	(95–)103(–114)
Themistoclesia epiphytica	+	100	(7–)13(–16)	−	+	−	+	−	−	(25–)30(–35)	(120–)153(–170)
T. pendula	+	0	0	−	+	−	+	−	−	(30–)61(–85)	(62–)75(–102)
T. vegasana	+	20	(1–)7(–11)	−	+	−	+	−	−	(15–)30(–45)	(130–)156(–192)
Thibaudia angustifolia	+	95	(1–)4(–9)	±	+	−	+	−	−	(20–)31(–40)	(125–)159(–230)
T. floribunda	+	30	(1–)6(–13)	−	+	−	+	−	−	(20–)36(–45)	(42–)64(–80)
T. formosa	?	90	(1–)7(–11)	−	+	−	+	−	−	(20–)34(–55)	(38–)70(–110)
T. jahnii	+	90	(1–)6(–10)	−	+	−	+	−	−	(20–)35(–45)	(76–)107(–141)
T. martiniana	?	100	(4–)8(–10)	−	+	−	+	−	−	(40–)53(–70)	(36–)69(–84)
T. pachypoda	+	35	(1–)4(–8)	−	+	−	+	−	−	(30–)43(–50)	(100–)144(–185)
T. parvifolia	?	95	(1–)7(–11)	−	+	−	+	−	−	(20–)25(–30)	(112–)141(–168)
T. rigidiflora	?	95	(1–)5(–13)	−	+	−	+	−	−	(30–)43(–60)	(64–)81(–100)
Vaccinium sp. indet.	?	50	(1–)8(–18)	±	+	−	−	+	−	(15–)23(–40)	(160–)228(–280)
V. africanum	?	75	(1–)8(–20)	±	+	−	+	+	−	(25–)32(–40)	(95–)138(–170)
V. angustifolium	−	80	(1–)8(–12)	+	+	+	−	+	−	(12–)18(–29)	(200–)267(–310)
V. arboreum	?	75	(7–)26(–53)	+	+	+	−	+	+	(18–)25(–40)	(89–)109(–150)
V. atrococcum	?	85	(4–)10(–16)	+	+	±	±	+	−	(15–)23(–35)	(170–)200(–240)
V. bancanum	?	0	0	±	+	+	−	−	−	(35–)46(–60)	(52–)65(–88)

Table 1. Extended. Continued.

Vessels	Tracheids	Fibers	Rays			Crystals	
Length of vessel elements (μm)	Length of tracheids (μm)	Length of fiber tracheids (μm)	Multiseriate ray width (number of cells)	Height of uniseriate rays (μm)	Height of multiseriate rays (μm)	Present in rays	Present in axial parenchyma
(580–)833(1080)	(850–)1069 (–1190)	(990–)1146 (–1300)	4–7	(400–)711(–1200)	1600->6000	+	–
(420–)637(–900)	(460–)713(–780)	(850–)1000 (–1180)	3–4	(250–)764(–1300)	(1300–)2793(–5400)	–	–
(300–)522(–650)	(400–)543(–660)	(600–)740(–900)	3	(250–)485(–90)	(800–)2845(–7000)	+	–
(490–)744(–990)	(650–)756(–850)	(900–)1150 (–1500)	5–6	(350–)644(–1200)	1900->9000	+	–
(640–)789 (–1000)	(840–)938 (–1100)	(800–)1053 (–1260)	9–14	(450–)881(–1500)	2700->12000	+	–
(570–)745(–930)	(630–)758(–810)	(870–)1004 (–1210)	4–8	(300–)647(–1450)	4000->11000	–	–
(430–)688(–800)	(620–)711(–800)	(780–)910(–1250)	5–8	(400–)700(–1600)	(1900–)2600(–3300)	+	–
(430–)649(–880)	(620–)685(–740)	(800–)912(–1000)	4–5	(400–)1456 (–1200)	(1450–)2983(–3950)	–	–
(270–)430(–510)	(450–)546(–730)	(500–)662(–810)	4–7	(200–)466(–900)	(600–)1013(–1950)	–	–
(370–)512(–600)	(390–)477(–570)	(540–)707(–930)	3	(450–)883(–1500)	1100->4100	+	–
(340–)452(–600)	(370–)457(–550)	(450–)586(–670)	5–8	(150–)402(–600)	(1200–)1668(–2300)	–	–
(400–)620(–800)	(400–)442(–520)	(630–)778(–950)	2–4	(250–)444(–600)	?	–	–
(420–)620(–850)	(430–)508(–650)	(800–)1010 (–1150)	4	(350–)564(–900)	(600–)1511(–2400)	–	–
(480–)696(–890)	(560–)648(–720)	(720–)888(–1050)	4–12	(900–)1406 (–1800)	>10.000	–	–
(280–)473(–730)	(520–)594(–720)	(650–)821(–930)	5–7	(400–)535(–850)	1500–>4900	+	+
(400–)538(–650)	(480–)593(–720)	(600–)766(–950)	3–5	(300–)538(–1100)	2400->6000	+	–
(570–)733(–930)	(600–)702) (–780)	(780–)881(–1050)	3–5	(700–)1459 (–3000)	(1200–)3350(–6300)	–	–
(410–)508(–680)	(570–)637(–690)	(630–)767(–830)	5–11	(200–)437(–650)	(950–)2123(–4500)	+	–
(350–)534(–800)	(430–)628(–920)	(700–)940(–1150)	5–7	(300–)527(–900)	(1200–)2475(–5500)	+	–
(330–)608(–850)	(580–)662(–760)	(760–)957(–1170)	4–5	(350–)850(–1450)	(1800–)2775(–6300)	+	+
(560–)836 (–1000)	(750–)891(–960)	(1000–)1177 (–1350)	3–4	(450–)929(–1500)	(1300–)2777(–4500)	+	–
(570–)763(–930)	(700–)851 (–1160)	(930–)1109 (–1270)	3–12	(500–)1000 (–1450)	(900–)3600(–6700)	+	+
(210–)539(–650)	(570–)628(–700)	(600–)783(–920)	4–6	(550–)830(–1150)	(1100–)2510(–2900)	–	–
(370–)636(–870)	(750–)790(–850)	(930–)1041 (–1170)	4–6	(350–)633 (–1800)	(1300–)2511(–5200)	+	+
(160–)393(–520)	(420–)455(–470)	(450–)523(–600)	3–4	(250–)421(–1050)	(550–)924(–1555)	–	–
(490–)649(–840)	(540–)590(–700)	(670–)835(–1070)	5–8	(450–)658(–900)	(950–)2046(–3200)	–	–
(210–)296(–390)	(300–)318(–350)	(390–)456(–520)	3–4	(250–)383(–750)	(350–)700(–1200)	–	–
(450–)642(–850)	(560–)764(–880)	(1100–)1324 (–1650)	5–6	(300–)556(–900)	(500–)1397(–2400)	–	–
(210–)381(–500)	(420–)467(–550)	(500–)690(–830)	4–6	(100–)243(–400)	(200–)730(–1400)	–	
(380–)696(–950)	(620–)824(–950)	(920–)1150 (–1370)	3–5	(200–)323(–450)	(450–)1458(–2050)	+	–

Table 1. Continued.

Species studied	Secretory ducts in pith or primary xylem	Vessels: Percentage of scalariform perforations	Number of bars	Opposite vessel-ray pitting	Scalariform vessel-ray pitting	Alternate vessel-ray pitting	Simple vessel-ray pitting	Helical thickening throughout vessel elements	Helical thickenings in fibers and/or tracheids	Tangential diameter of vessel lumina (μm)	Vessels per square mm
V. barandanum var. *barandanum*	?	20	(1–)3(–5)	+	+	–	±	–	–	(30–)40(–50)	(31–)53(–65)
V. berberidifolium	–	90	(9–)12(–14)	±	+	+	–	+	–	(11–)16(–21)	(240–)294(–210)
V. bracteatum	?	50	(6–)9(–13)	+	+	–	±	+	–	(20–)32(–50)	(165–)210(–260)
V. calycinum	?	90	(1–)15(–33)	±	+	–	–	–	–	(20–)25(–40)	(190–)242(–360)
V. consanguineum	?	25	(5–)13(–15)	+	+	+	±	+	–	(30–)38(–45)	(81–)107(–124)
V. corymbodendron	?	80	(4–)12(–18)	+	+	+	±	–	–	(20–)30(–40)	(76–)106(–126)
V. corymbosum	–	80	(2–)9(-19)	±	+	–	–	+	–	(12–)16(–22)	(380–)430(–495)
V. cumingianum	?	5	(1–)3(–5)	±	+	–	±	–	–	(15–)30(–45)	(72–)79(–88)
V. exaristatum	?	50	(2–)8(–15)	±	+	–	±	–	–	(30–)38(–50)	(52–)73(–102)
V. exul	?	80	(3–)8(–12)	+	–	+	–	–	–	(23–)42(–60)	(42–)61(–83)
V. floccosum	?	30	(3–)6(–9)	±	+	–	–	–	–	(25–)37(–60)	(82–)103(–140)
V. floribundum	—	90	(1–)9(–18)	+	+	+	–	+	–	(10–)14(–20)	(280–)334(–380)
V. globulare	?	0	0	±	–	+	–	+	+	(15–)19(–30)	(160–)297(–360)
V. leschenaultii	?	40	(2–)9(–14)	+	±	+	–	–	–	(25–)34(–40)	(66–)83(–100)
V. leucanthum	?	60	(1–)7(–10)	+	±	+	–	+	–	(15–)31(–40)	(92–)107(–128)
V. maderense	?	75	(1–)3(–6)	±	+	–	–	+	–	(15–)25(–35)	(170–)210(–240)
V. membranaceum	?	85	(6–)11(–16)	+	+	–	–	+	–	(15–)21(–30)	(220–)273(–360)
V. meridionale	?	0	0	±	–	+	–	–	–	(70–)83(–105)	(20–)23(–26)
V. myrtillus	—	90	(5–)10(–14)	+	+	–	–	–	–	(15–)18(–25)	(285–)344(-400)
V. occidentale	?	60	(4–)8(–11)	+	–	+	–	–	–	(13–)18(–25)	(290–)403(–448)
V. ovatum	?	100	(8–)12(–15)	+	+	–	±	+	+	(15–)22(–30)	(200–)238(–289)
V. parvifolium	?	100	(6–)9(–12)	+	+	–	–	+	–	(15–)17(–20)	(210–)263(–300)
V. puberulum var. *subcrenulatum*	?	90	(2–)6(–11)	±	+	–	±	–	–	(25–)32(–40)	(80–)100(–120)
V. scoparium	?	50	(2–)4(–8)	+	+	–	–	–	–	(12–)16(–25)	(310–)336(–390)
V. stanleyi	–	70	(2–)7(–10)	±	+	–	±	–	–	(15–)21(–30)	(250–)280(–310)
V. uliginosum	–	15	(1–)4(–6)	+	–	+	–	–	–	(10–)14(–20)	(360–)421(–480)

Table 1. Extended. Continued.

Vessels	Tracheids	Fibers	Rays			Crystals	
Length of vessel elements (μm)	Length of tracheids (μm)	Length of fiber tracheids (μm)	Multiseriate ray width (number of cells)	Height of uniseriate rays (μm)	Height of multiseriate rays (μm)	Present in rays	Present in axial parenchyma
(470–)695(–960)	(430–)663(–830)	(860–)999(–1120)	4–7	(200–)400(–650)	(500–)1217(–1800)	–	–
(370–)517(–650)	(430–)507(–570)	(510–)648(–810)	2–5	(400–)583(–800)	(700–)986(–1600)	–	–
(300–)487(–600)	(470–)687(–970)	(900–)1081(–1300)	5–6	(350–)563(–1100)	(700–)1408(–3000)	–	–
(270–)422(–520)	(390–)508(–600)	(450–)598(–700)	3–4	(150–)286(–450)	(300–)617(–1100)		
(520–)721(–920)	(700–)776(–850)	(840–)1042(–1210)	4–5	(250–)554(–1200)	(400–)1059(–1600)	–	–
(450–)640(–850)	(440–)650(–800)	(750–)965(–1100)	5–7	(250–)441(–600)	(800(–)1079(–1500)	–	–
(200–)298(–400)	(310–)368(–520)	(350–)526(–650)	3	(200–)486(–1150)	(500–)1388(–4200)	+	–
(410–)596(–830)	(500–)644(–750)	(840–)930(–1160)	5–7	(400–)586(–900)	(800–)1837(–3300)	+	–
(360–)539(–690)	(430–)678(–830)	(680–)943(–1170)	4–7	(250–)463(–1050)	(400–)1055(–2100)	–	–
(570–)910(–1170)	(890–)942(–1050)	(1020–)1408(–1970)	6–12	(350–)750(–1100)	(800–)1725(–3700)	–	–
(370–)907(–830)	(530–)640(–720)	(900–)1108(–1133)	3–6	(450–)886(–1700)	(900–)2661(–6800)	–	–
(360–)389(–880)	(290–)423(–490)	(440–)549(–670)	5–7	(150–)275(–450)	(500–)728(–850)		
(260–)387(–570)	(300–)383(–520)	(330–)435(–520)	?	?	?	–	–
(520–)737(–930)	(750–)942(–1020)	(1020–)1198(–1450)	1–6	(300–)585(–1050)	(1000–)1710(–2500)	+	–
(320–)536(–880)	(450–)506(–600)	(830–)1043(–1250)	3-6	(350–)522(–700)	(500–)868(–1200)	–	-
(250–)448(–570)	(400–)545(–510)	(480–)622(–740)	4–9	(200–)275(–400)	(450–)933(–1300)	–	–
(230–)366(–470)	(200–)250(–280)	(370–)493(–580)	3	(300–)479(–750)	(500–)643(–1050)		
(430–)739(–1040)	(900–)1013(–1150)	(1320–)1516(–1800)	4–5	(350–)581(–1050)	(750–)1844(–3900)	+	–
(300–)471(–580)	(220–)300(–350)	(370–)564(–680)	4–5	(200–)305(–400)	(350–)725(–950)		–
(150–)220(–320)	(140–)210(–250)	(220–)302(–380)	3–4	(150–)263(–350)	(350–)685(–1150)	–	–
(330–)558(–800)	(270–)394(–520)	(630–)771(–950)	4–5	(500–)610(–800)	(650–)912(–1500)	+	
(300–)403(–510)	(270–)414(–560)	(450–564(–710)	2–3	(300–)383(–500)	(350–)538(–950)	–	–
(570–)697(–860)	(350–)450(–600)	(890–)1042(–1340)	4–5	(450–)715(–1200)	(1100–)1930(–2700)	+	–
(170–)256(–400)	(200–(251(–280)	(280–)330(–370)	3	(150–)207(–300)	(250–)475(–650)	–	–
(230–)438(–600)	(480–)522(–620)	(680)–)783(–1030)	4–5	(250–)367(–650)	(500–)1045(–1700)	–	–
(130–)242(–350)	(270–)341(–410)	(370–)400(–450)	4–5	(200–)275(–400)	(400–)575(–1050)	–	–

be rather arbitrary to distinguish intermediate cell types to one of these categories, because their definition remains a matter of dispute (Baas, 1986; Carlquist, 2001). Therefore, we prefer to give a detailed description of these cells. We consider tracheids to be long and narrow cells, with dense pitting in tangential walls (more than 15 pits per 100 μm of tracheid length) and radial walls (more than 20 pits per 100 μm of tracheid length). These pits are distinctly bordered and form two or three longitudinal rows in the radial and tangential walls (see Fig. 3H). Fiber-tracheids represent the most common cell type of the ground tissue. They are somewhat longer than tracheids, narrow, thin- or thick-walled, and contain one single row of distinctly bordered pits in tangential walls (ca. 5 to 15 pits per 100 μm of fiber-tracheid length) and radial walls (ca. 5 to 20 pits per 100 μm of fiber-tracheid length). The mean distance between two fiber-tracheid pits in the tangential wall is longer than the distance between two tracheid pits, although the pit borders do not differ in size (ca. 3–6 μm). Libriform fibers are generally as long as fiber-tracheids. They are narrow, mostly thin-walled and septate, and show few to very few, minutely bordered to simple pits in the tangential walls. The pit borders in the libriform fibers are 2–3 μm in size, and their density ranges from less than 1 to 4 per 100 μm of length in tangential walls, and from 2 to about 10 per 100 μm of length in radial walls. Sometimes only two or three pits are observed near the end of libriform fibers. Septate fiber-tracheids and intermediate cells between septate libriform fibers and fiber-tracheids are also seen in most species. For all measurements of tracheary elements, only clearly identifiable cells were taken into account.

Wood features were plotted on trees using the program MacClade 4.04 (Maddison & Maddison, 2002).

Results

Woods of most species have indistinct growth rings and are diffuse-porous (Figs. 1, 2), although a few species of *Cavendishia*, *Satyria* Klotzsch, *Thibaudia* J. St.-Hil., and *Vaccinium* (Fig. 1C) show a tendency to semi-ring-porous wood. Vessels are angular and mainly solitary (Figs. 1, 2), although some tangential vessel groupings of 2 to 4 cells are reported in several genera. The mean tangential vessel diameter ranges from 14 μm in *Vaccinium uliginosum* to 164 μm in *Dimorphanthera kempteriana* with an overall average of 35 μm. Likewise, the two species mentioned show extreme mean vessel density values (421 and 12 vessels per square mm, respectively), while the mean value for the entire tribe is 145 vessels per square mm. The mean length of the vessel elements is 600 μm and varies from 220 μm in *Vaccinium occidentale* to 1006 μm in *Disterigma cryptocalyx*.

Vaccinieae often have mixed simple and scalariform perforation plates, although the scalariform type usually dominates. Genera with species having mostly scalariform perforations include *Anthopterus* Hook., *Ceratostema* Juss., *Demosthenesia* A. C. Sm., *Diogenesia* Sleumer, *Disterigma* (Klotzsch) Nied., *Lateropora* A. C. Sm., *Gaylussacia*, *Mycerinus* A. C. Sm., *Plutarchia* A. C. Sm., *Oreanthes* Benth. (Fig. 3D), *Orthaea* Klotzsch (Fig. 3C), *Semiramisia* Klotzsch, *Symphysia* C. Presl, and *Sphyrospermum* Poepp. & Endl., while simple perforations dominate in *Dimorphanthera* F. Muell., *Notopora* Hook. f., *Polyclita* A. C. Sm., and *Siphonandra* Klotzsch; the other genera show more variation in the type of vessel perforation between the species observed, for example, *Agapetes* (Figs. 3A, E) and *Vaccinium* (Figs. 3B, F). Intervessel pits are scarce and mostly opposite (2–5 μm in size) to scalariform (6–20 μm in size), except in *Agapetes* and *Vaccinium*, which often show alternate intervessel pitting (2–5 μm in size). Vessel-ray pits are scalariform with strongly reduced borders in most genera (Figs. 4E–H) except for *Agapetes*, *Gaylussacia*, and most *Vaccinium* species, and range from rather small (6 μm in size) to very large (40 μm in size in species with wide vessels). Alternate vessel-ray pits with distinct borders are typical of *Agapetes* (2–5 μm in size, Fig. 4D), while in *Vaccinium* all types of vessel-ray pitting is observed.

Helical thickenings are nearly always present in the tails of vessel elements; their presence throughout the body of vessel elements is restricted to species of *Agapetes*, *Disterigma*, *Ceratostema*, *Gaylussacia*, and is especially common in *Vaccinium* (Fig. 3G). Helical thickenings were also observed in some fibers and/or tracheids of *Agapetes*, *Disterigma*, and *Vaccinium*.

The ground tissue of the wood consists of fiber-tracheids, except for *Dimorphanthera collinsii*, *D. cornuta*, and *Macleania rupestris*, in which tracheids form the ground tissue. The fiber-tracheids have very thin to thick walls. The mean length of the fiber-tracheids is 865 μm with a minimum mean value of 302 μm in *Vaccinium occidentale* and a maximum mean length of 1516 μm in *Vaccinium meridionale*. Occasionally thin-walled libriform fibers, which are usually septate with few simple to indistinctly bordered pits, were reported in all species, except for *Dimorphanthera kempteriana*, *Macleania crassa*, *M. rupestris*, *Satyria* sp. in-

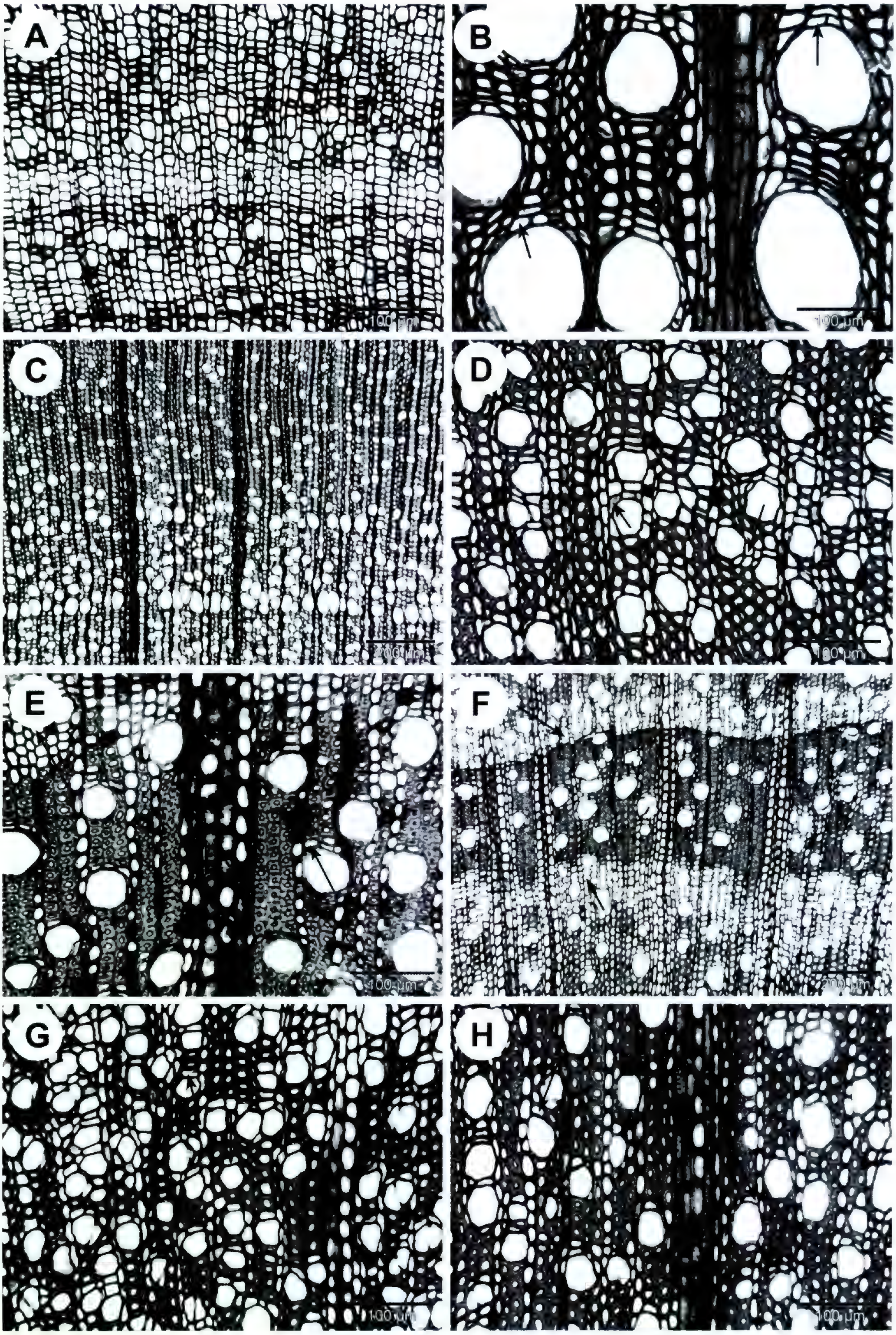

Figure 1. A–H. Transverse sections showing arrangement of vessels, distribution of axial parenchyma (arrows), and thickness of fiber walls. —A. *Agapetes flava* (*Grierson & Long 3076*, E 19822403). —B. *Dimorphanthera dekockii* var. *pubiflora* (*Vink 17307*, Kw 11639). —C. *Vaccinium calycinum* (*Stern 2950*, Tw 24121). —D. *Vaccinium puberulum* var. *subcrenulatum* (*Maas et al. 5733*, Uw 27342). —E. *Notopora schomburgkii* (*Maas et al. 5808*, Uw 27397). —F. *Psammisia* cf. *ulbrichiana* (*Luteyn & Lebrón-Luteyn 6532*, NY). —G. *Lateropora ovata* (*Luteyn 15294*, NY). —H. *Diogenesia tetrandra* (*Luteyn et al. 7388*, NY).

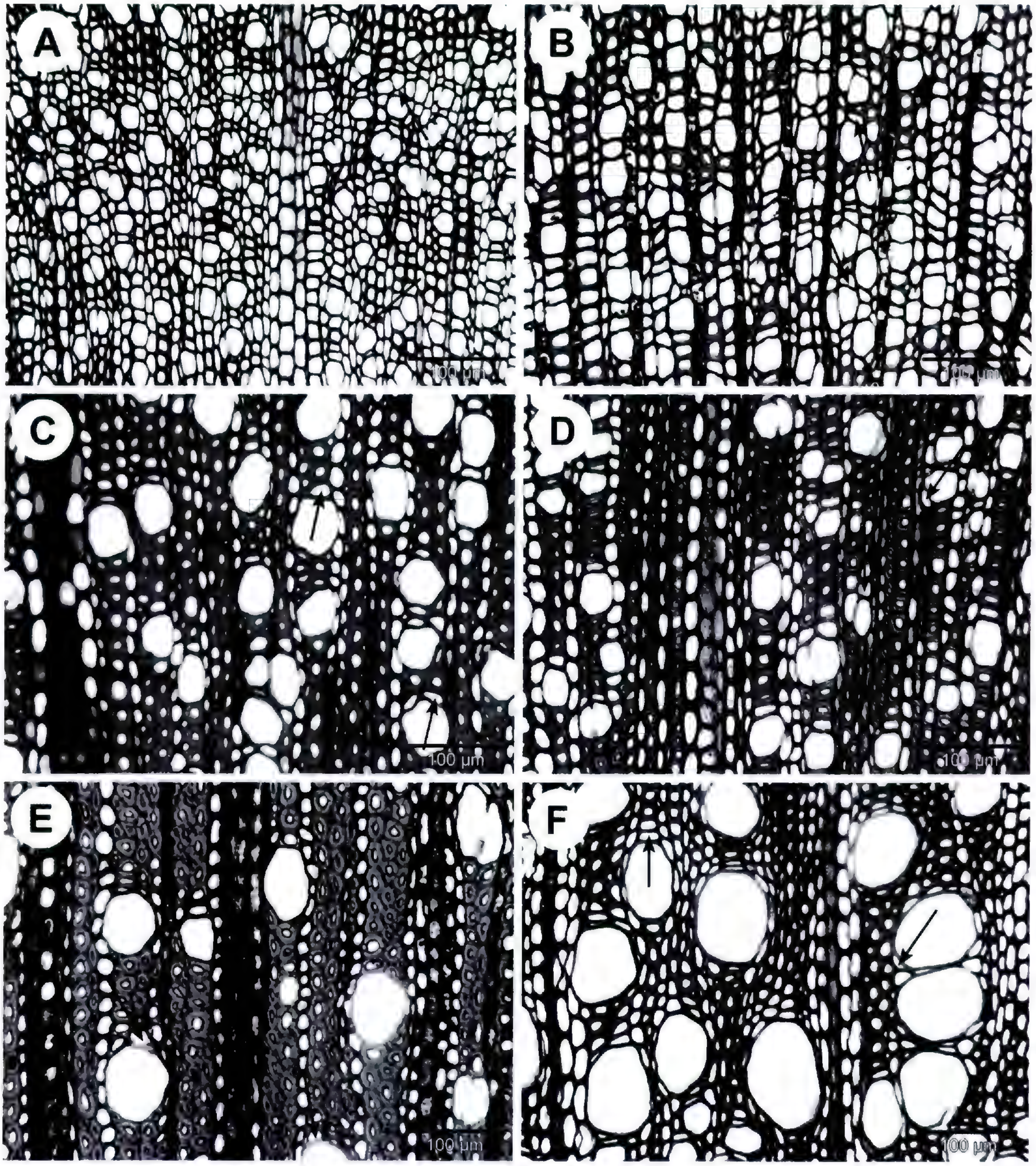

Figure 2. A–F. Transverse sections showing arrangement of vessels, distribution of axial parenchyma (arrows), and thickness of fiber walls. —A. *Sphyrospermum* sp. indet. (*Argent*, E 19762390). —B. *Demosthenesia spectabilis* (*Luteyn 6452*, NY). —C. *Cavendishia bracteata* (*Dorr et al. 6890*, Lw). —D. *Macleania stricta* (*Luteyn & Lebrón-Luteyn 5744*, NY). —E. *Orthaea fimbriata* (*Luteyn & Lebrón-Luteyn 5794*, NY). —F. *Satyria meiantha* (*Breedlove 9746*, MADw 23933).

det. (Uw 17005), *Siphonandra elliptica*, *Themistoclesia pendula*, *T. vegasana*, and *Vaccinium meridionale*. The libriform fibers are somewhat shorter than fiber-tracheids (on average 700 µm) and contain nuclei (Fig. 5H). Also septate fiber-tracheids and cells intermediate between septate libriform fibers and fiber-tracheids were observed in most species. In general, tracheids are present (Fig. 3H), although they were not observed in *Disterigma cryptocalyx*, *Vaccinium membranaceum*, *V. myrtillus*, *V. occidentale*, and *V. puberulum*. In *Dimorphanthera collinsii* and *D. cornuta*, the ground tissue is formed by tracheids only, which show large, bordered pits usually between 6 and 9 µm in size.

The main distribution type of the axial paren-

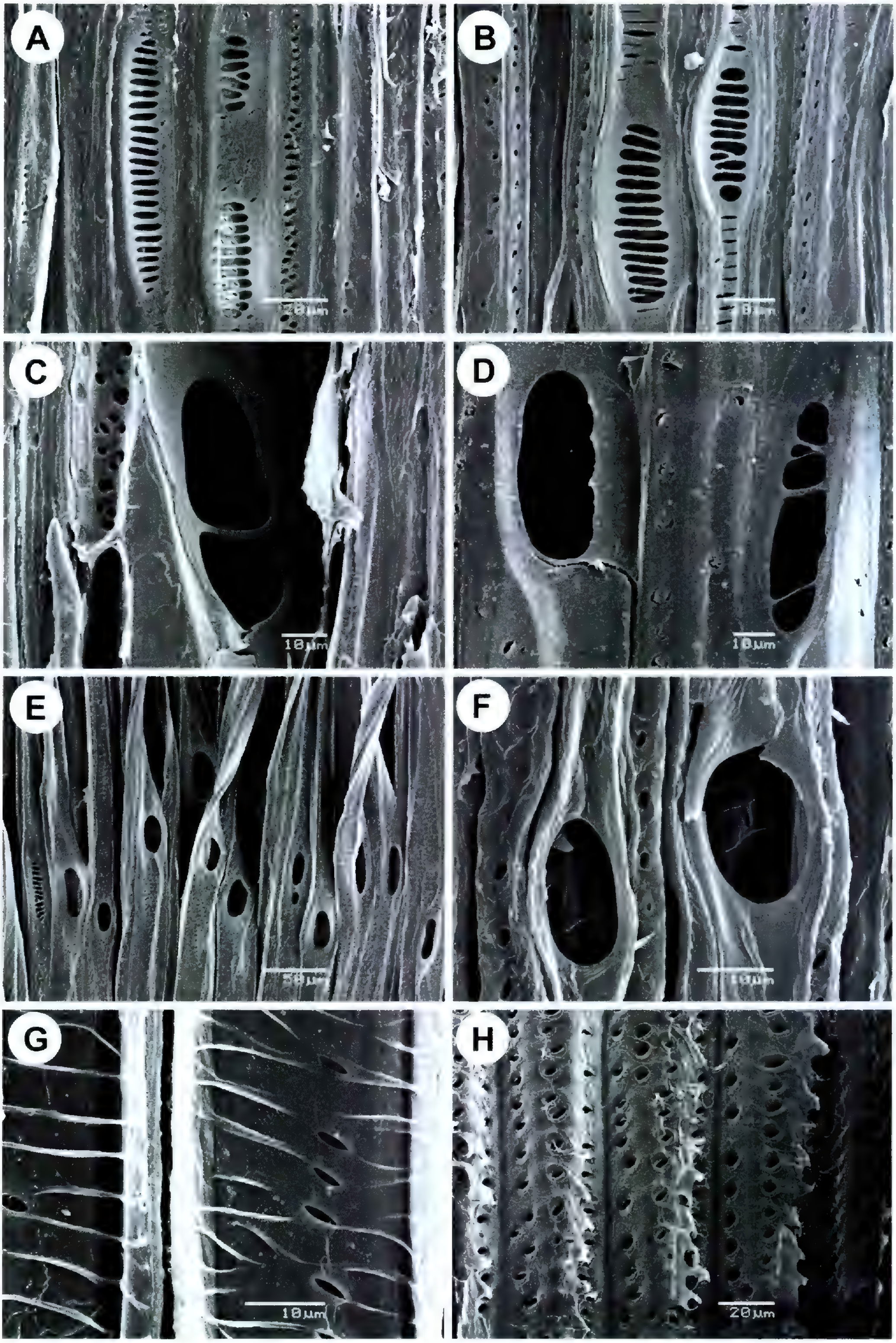

Figure 3. A–C. Scalariform vessel perforations. —A. *Agapetes hosseana* (*Burtt 958*, E 19672592). —B. *Vaccinium angustifolium* (*Lens*, BR). —C. *Orthaea fimbriata* (*Luteyn & Lebrón-Luteyn 5794*, NY). —D. Vessel perforation mixed scalariform and simple: *Oreanthes ecuadorensis* (*Luteyn 15394*, NY). E–F. Simple vessel perforations. —E. *Agapetes sikkimensis* (*Sinclair & Long 5778*, E 19842032). —F. *Vaccinium globulare* (*Dechamps 4460*, Tw 46335). —G. Helical thickenings throughout vessel element: *Vaccinium oratum* (*Dechamps 4418*, Tw 46267). —H. Tracheids: *Dimorphanthera kempteriana* (*Vink 16888*, Tw 23733).

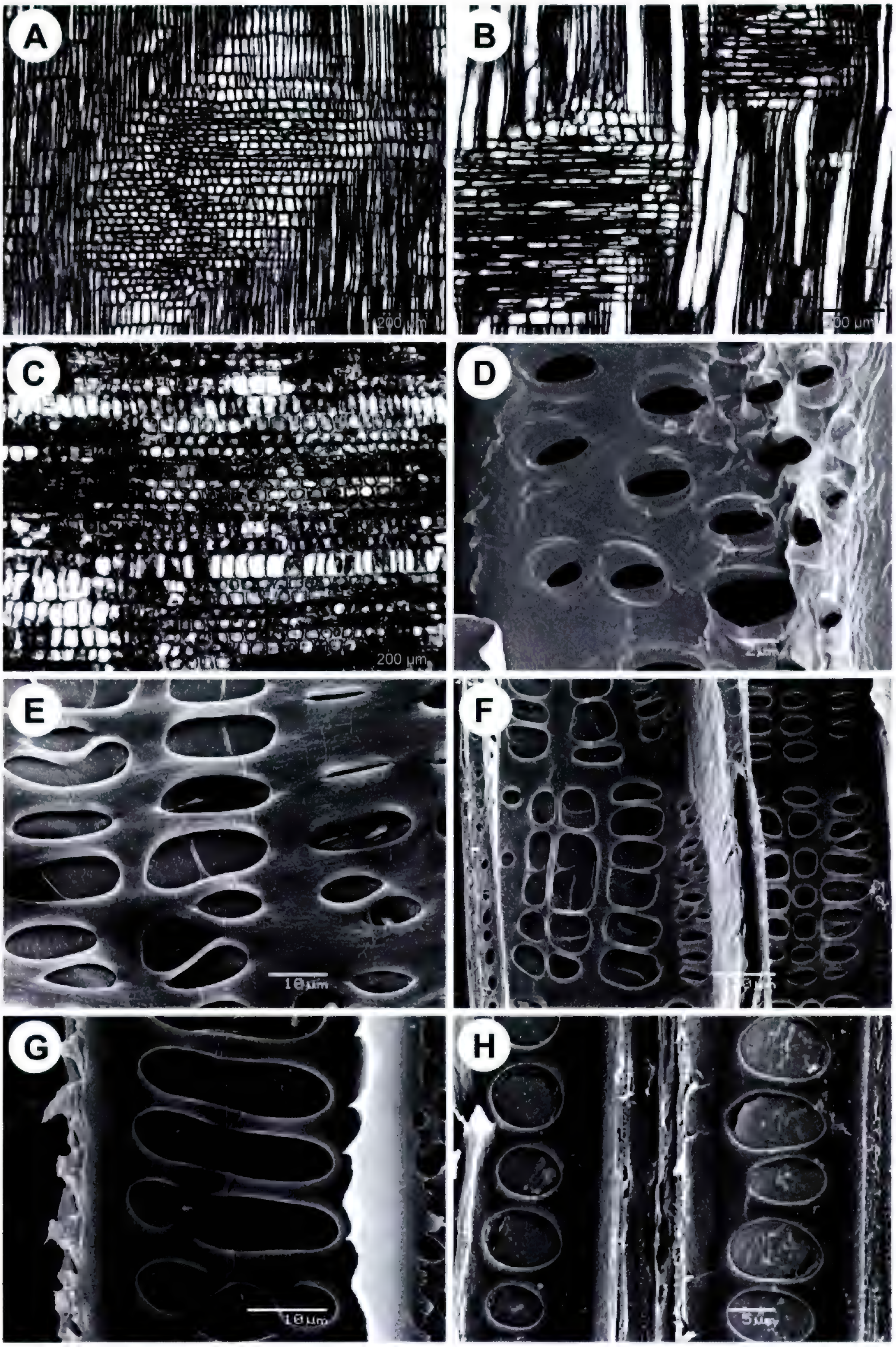

Figure 4. A–C. Radial sections showing structure of multiseriate rays. —A. Procumbent, square and upright body ray cells: *Agapetes mannii* (*Kingdon-Ward 19097*, E 19500046). —B. Exclusively procumbent body ray cells: *Vaccinium consanguineum* (*Wiemann 13*, Uw 30897). —C. Mainly upright and square body ray cells: *Macleania pentaptera* (*Luteyn & Lebrón-Luteyn 6957*, NY). D–H. Vessel-ray pitting. —D. Vessel-ray pits bordered: *Agapetes sikkimensis* (*Sinclair & Long 5778*, E 19842032). E–H. Vessel-ray pitting scalariform with much reduced borders. —E. *Dimorphanthera kempteriana* (*Vink 16888*, Tw 23733). —F. *Orthaea fimbriata* (*Luteyn & Lebrón-Luteyn 5794*, NY). —G. *Macleania loeseneriana* (*Luteyn & Lebrón-Luteyn 5726*, NY). —H. *Oreanthes ecuadorensis* (*Luteyn 15394*, NY).

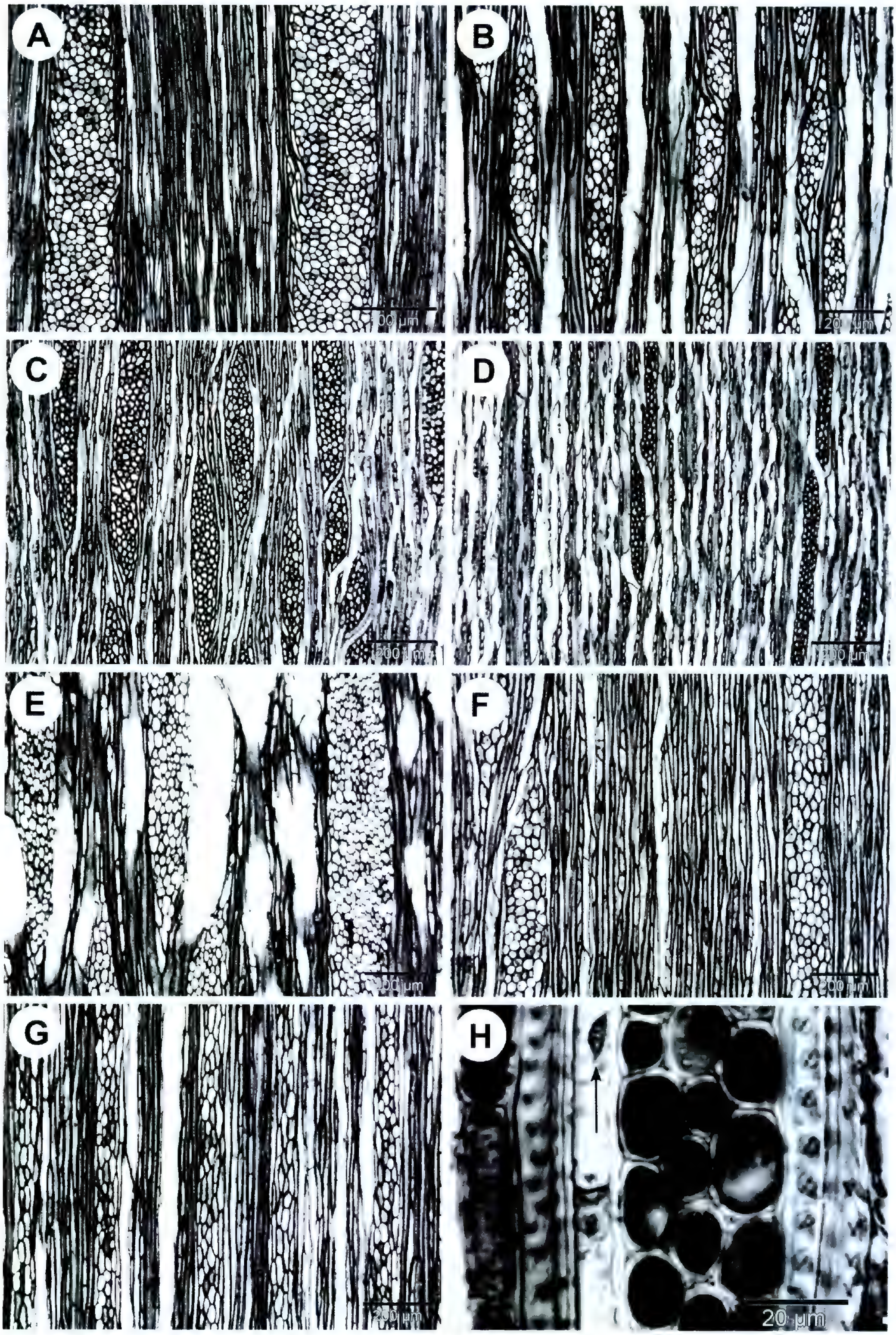

Figure 5. Tangential sections showing the width of multiseriate rays. —A. *Agapetes flava* (*Grierson & Long 3076*, E 19822403). —B. *Vaccinium barandanum* var. *barandanum* (*Jacobs 7249*, Uw 33743). —C. *Vaccinium floribundum* (*De Sloover 399*, BR). —D. *Vaccinium uliginosum* (*Dechamps 6033*, Tw 38581). —E. *Satyria* sp. indet. (*Maguire et al. 48650*, Uw 16976). —F. *Polyclita turbinata* (*Luteyn 15453*, NY). —G. *Psammisia* cf. *ulbrichiana* (*Luteyn & Lebrón-Luteyn 6532*, NY). —H. Nucleus (arrow) in septate libriform fiber: *Gaylussacia baccata* (*F. Lens*, BR).

chyma is scanty paratracheal (Figs. 1, 2); sparsely diffuse apotracheal parenchyma was also seen in species of *Agapetes*, *Cavendishia*, *Ceratostema*, *Dimorphanthera*, *Orthaea*, *Psammisia*, *Satyria*, *Thibaudia*, and *Vaccinium*, while diffuse-in-aggregates parenchyma was observed in some *Vaccinium* species. Banded marginal parenchyma was seen in a few species, viz. *Agapetes flava* (Fig. 1A), *Mycerinus chimantensis*, *Notopora schomburgkii*, *Psammisia* cf. *ulbrichiana* (Fig. 1F), *Satyria* sp. indet. (*Luteyn & Lebrón-Luteyn 7177*, NY), and *Sphyrospermum* sp. indet. Axial parenchyma strands usually consist of 2 to 4 cells, although strands with up to 8 cells were also observed. In almost all genera, except for *Gaylussaccia* and most species of *Vaccinium*, undivided (fusiform) axial parenchyma cells were seen, ranging from 350 μm to 1050 μm with an average length of 600 μm. Intermediate types between fusiform axial parenchyma cells and libriform fibers also occur.

Uniseriate rays consist of predominantly upright cells. The mean height of the uniseriate rays varies greatly from 207 μm in *Vaccinium uliginosum* to 2478 μm in *Psammisia graebneriana*, with an average height of 740 μm for all species studied. Chambered cell types and prismatic crystals are always absent within uniseriate rays.

Multiseriate rays are heterocellular and usually consist of procumbent, square and/or upright body ray cells and several rows of upright marginal ray cells. In *Agapetes*, *Dimorphanthera*, *Disterigma*, *Gaylussacia*, and *Vaccinium*, however, upright body ray cells are rare while procumbent and/or square body ray cells dominate (Figs. 4A, B). Multiseriate rays are in general 3 to 7 cells wide (Fig. 5). Narrow rays (2- to 3-seriate) were observed in juvenile stems of *Cavendishia compacta*, *Macleania ericae*, and *Mycerinus chimantensis*, while wide multiseriate rays (sometimes more than 10 cells wide) were seen in several *Agapetes* species (Fig. 5A) and in *Dimorphanthera dekockii*, *Disterigma alaternoides*, *Satyria panurensis*, *Themistoclesia epiphytica*, *Thibaudia floribunda*, *Thibaudia pachypoda*, and *Vaccinium exul*. Multiseriate rays are much higher than uniseriate rays, mostly between 1000 and 7500 μm, with an average height of 4020 μm. Multiseriate rays in some species are without doubt much higher than indicated by the measurements in Table 1, since the height of the multiseriate rays often exceeds the length on the section. Very high rays (more than 10,000 μm) were observed in species of *Agapetes*, *Disterigma*, *Macleania*, *Psammisia*, *Satyria*, and *Themistoclesia* Klotzsch. Sheath cells are mostly present, but not always clearly developed. Gummy deposits (possibly tannins) were frequently noticed in the ray cells (Figs. 4B, C, 5H).

Prismatic crystals occur in non-chambered ray cells (Fig. 6A) or in chambered ray cells (Figs. 6B, C), but they were absent in species investigated of *Ceratostema*, *Demosthenesia*, *Diogenesia*, *Gaylussacia*, *Oreanthes*, *Plutarchia*, *Semiramisia*, *Siphonandra*, and *Symphysia*. Sometimes they are observed in chambered axial parenchyma cells of *Anthopterus*, *Cavendishia*, *Disterigma*, *Macleania* (Fig. 6E), *Psammisia* (Fig. 6D), *Themistoclesia*, and *Thibaudia*.

The pith structure of the Vaccinieae species investigated is homogeneous. In *Demosthenesia*, *Gaylussacia*, *Oreanthes*, *Plutarchia*, and *Symphysia* no crystals were observed in the pith, but the remaining genera show prismatic crystals and/or druses. In *Notopora cardonae* and *Polyclita turbinata* (Fig. 6I), thick-walled sclereids are observed among the pith cells. Secretory ducts at the border of the primary xylem and the pith, but sometimes also in the pith, were observed in species of *Cavendishia*, *Demosthenesia*, *Diogenesia*, *Lateropora*, *Macleania*, *Oreanthes* (Fig. 6H), *Orthaea* (Fig. 6F, G), *Polyclita*, *Psammisia*, *Satyria*, *Semiramisia*, *Themistoclesia*, and *Thibaudia*.

Discussion

Our wood anatomical observations largely agree with the earlier description of Vaccinieae by Metcalfe and Chalk (1950), although some differences can be found. For instance, the width of the vessels is generally reported to be between 25 and 50 μm and only slightly larger in *Paphia*. We have observed several species with a mean tangential vessel diameter of more than 80 μm. Furthermore, Metcalfe and Chalk (1950) mentioned that helical thickenings throughout vessel elements are restricted to *Vaccinium*, but this study has shown that these thickenings are also present in species of *Agapetes*, *Ceratostema*, *Disterigma*, and *Gaylussacia*. In addition, helical thickenings are found throughout fiber-tracheids and/or tracheids in *Agapetes mannii*, *Disterigma* sp. indet., *Vaccinium arboreum*, *V. globulare*, and *V. ovatum*. The above-mentioned authors also underestimated the height of the multiseriate rays (commonly more than 1000 μm), but Giebel (1983) found a more correct value for the height of multiseriate rays in *Cavendishia*, i.e., often between 1073 and 7021 μm. The most striking new character is the observation of secretory ducts in the primary xylem and pith of 13 genera belonging to the Andean clade, which has not been recorded previously as far as we know. The

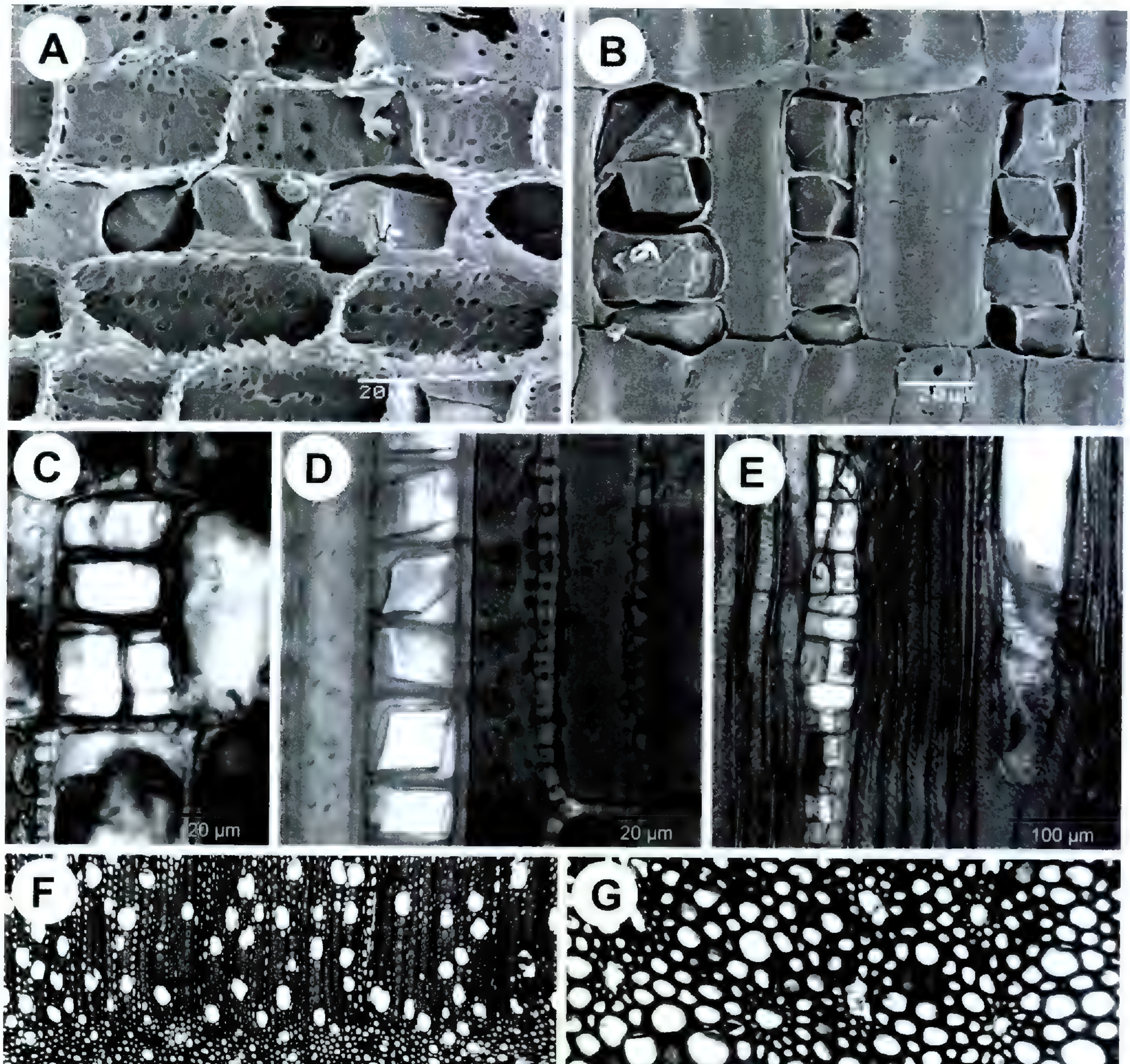

Figure 6. A–C. Prismatic crystals in ray cells. —A. Non-chambered ray cells: *Dimorphanthera kempteriana* (*Vink 16888*, Tw 23733). B, C. Chambered ray cells. —B. *Mycerinus chimantensis* (*O. Huber 9010*, NY). —C. *Notopora schomburgkii* (*Maas et al. 5808*, Uw 27397). D, E. Prismatic crystals in chambered axial parenchyma cells. —D. *Psammisia* sp. indet. (*van Rooden et al. 359*, Uw 25565). —E. *Macleania crassa* (*Luteyn et al. 7378*, NY). F–H. Secretory ducts in primary xylem and pith. —F, G. Transverse section (arrows): *Orthaea fimbriata* (*Luteyn & Lebrón-Luteyn 5794*, NY). —H. Longitudinal section showing secretory cells (arrows) around a secretory duct (SD): *Oreanthes ecuadorensis* (*Luteyn 15394*, NY). —I. Sclereids in pith: *Polyclita turbinata* (*Luteyn 15453*, NY).

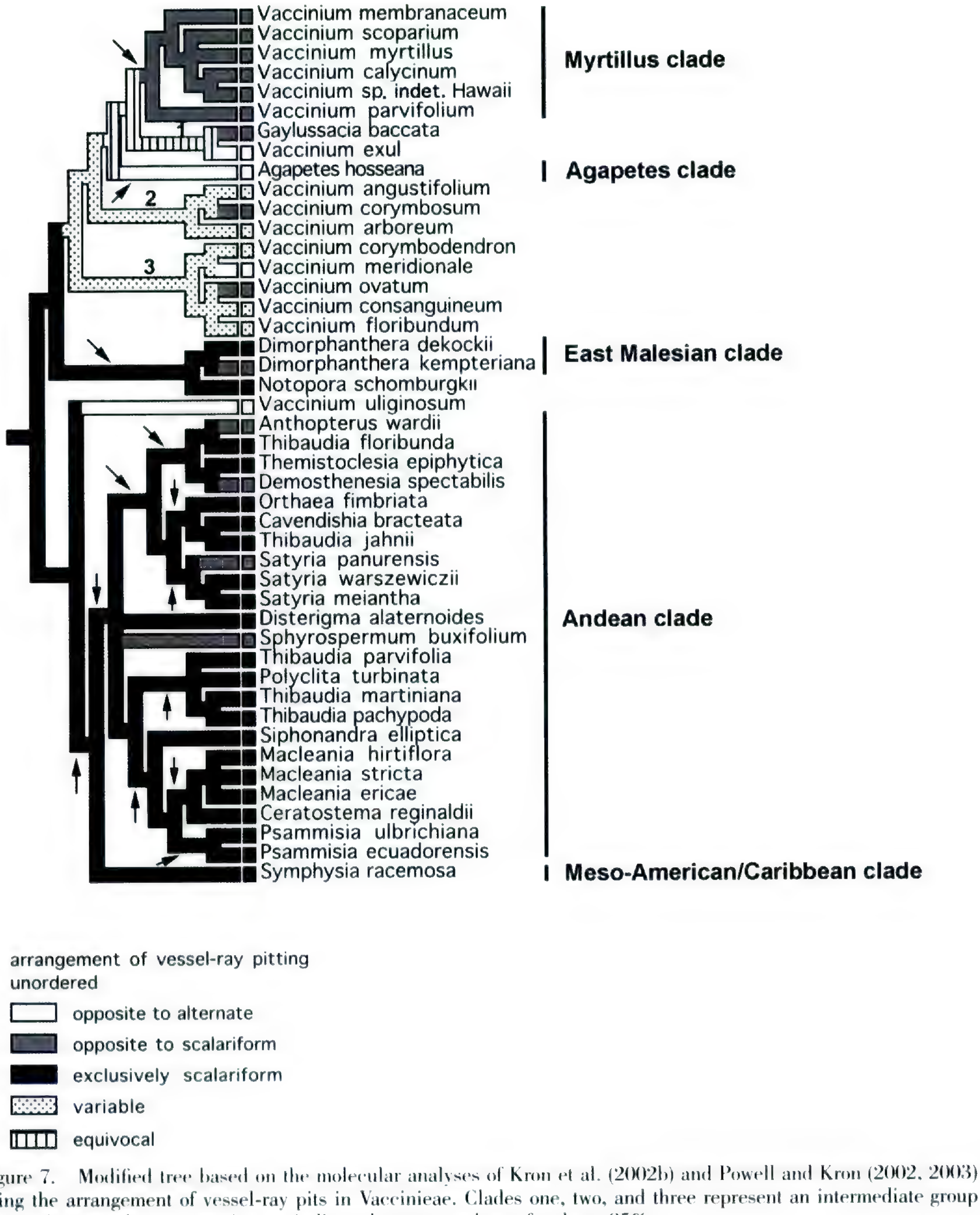

Figure 7. Modified tree based on the molecular analyses of Kron et al. (2002b) and Powell and Kron (2002, 2003) showing the arrangement of vessel-ray pits in Vaccinieae. Clades one, two, and three represent an intermediate group based on their wood structure. Arrows indicate bootstrap values of at least 85%.

exact contents of these secretory ducts is unknown. When unbleached, longitudinal sections were observed, a brown substance was sometimes seen, but the secretory duct also seems to be empty in many cases (Fig. 6H). It is also unclear whether these secretory ducts are present in other vegetative tissues.

We also found nuclei in septate libriform fibers of the two species that were stored in FAA, namely *Gaylussacia baccata* and *Vaccinium angustifolium*. Besides these two species, it is known that other Vaccinieae species contain living fibers, namely *Vaccinium myrtillus*, *V. varingiaefolium*, and species of *Cavendishia* (Wolkinger, 1970; Giebel, 1983). It is generally accepted that nuclei in septate fibers persist much longer than in fiber-tracheids and tracheids. Nuclei in septate fibers are likely to be found in Vaccinieae, if fresh material

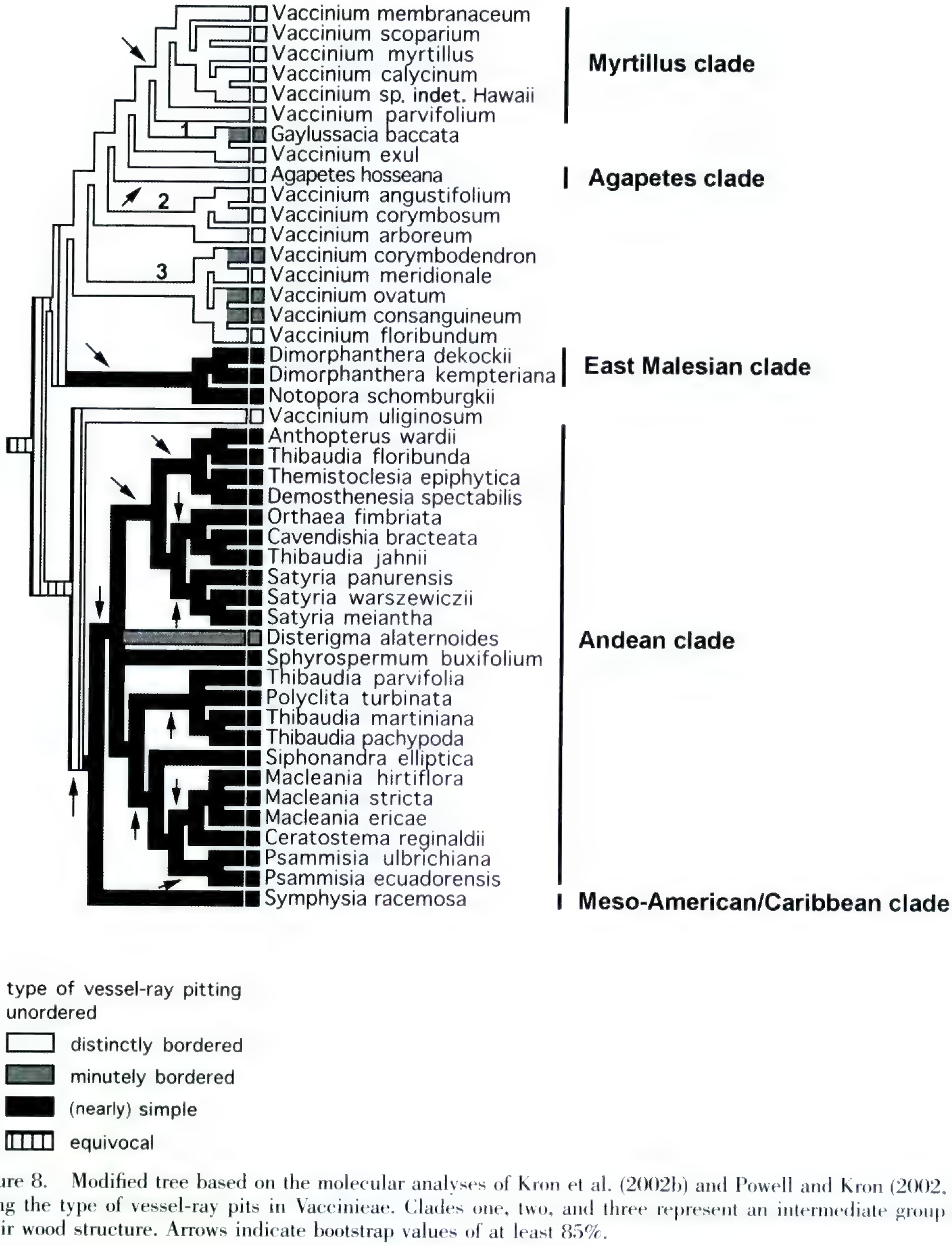

Figure 8. Modified tree based on the molecular analyses of Kron et al. (2002b) and Powell and Kron (2002, 2003) showing the type of vessel-ray pits in Vaccinieae. Clades one, two, and three represent an intermediate group based on their wood structure. Arrows indicate bootstrap values of at least 85%.

is preserved in FAA. Since Vaccinieae and the subfamily Vaccinioideae as a whole is characterized by septate fibers, it is expected that nucleate fibers are typical of the subfamily. Indeed, several authors have noticed the presence of living fibers in Vaccinieae (Braun, 1961; Fahn & Leshem, 1962; Giebel, 1983) and other tribes of the subfamily (Lens et al., 2004a). However, there are also records in Arbutoideae, another subfamily of Ericaceae, in which septate fibers are found (Wolkinger, 1970).

PHYLOGENETIC WOOD ANATOMY

In order to comment on the recent generic realignments within the tribe and to trace the evolution of some important wood anatomical characters, we have created a tree, based on the molecular phylogenetic studies of Kron et al. (2002b) and

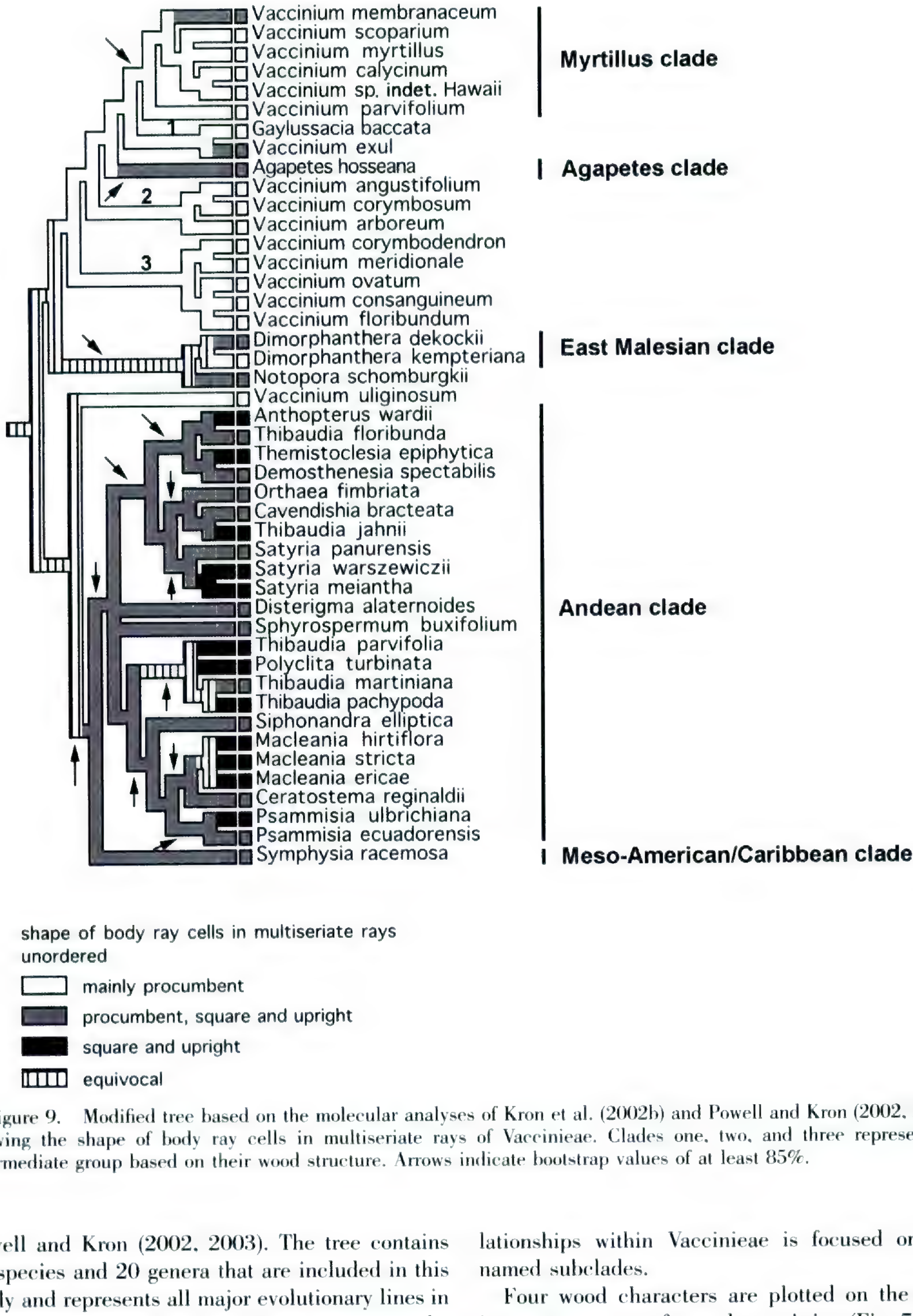

Figure 9. Modified tree based on the molecular analyses of Kron et al. (2002b) and Powell and Kron (2002, 2003) showing the shape of body ray cells in multiseriate rays of Vaccinieae. Clades one, two, and three represent an intermediate group based on their wood structure. Arrows indicate bootstrap values of at least 85%.

Powell and Kron (2002, 2003). The tree contains 45 species and 20 genera that are included in this study and represents all major evolutionary lines in Vaccinieae, except for the Bracteata–Oarianthe clade. This clade, comprised of species of *Vaccinium* from New Guinea and Borneo, was omitted from this study due to lack of material. As indicated by arrows, the subclades with an informal name have bootstrap values of at least 85%, but relationships between these clades are poorly supported (Figs. 7–10). Therefore, our discussion of the relationships within Vaccinieae is focused on the named subclades.

Four wood characters are plotted on the tree, i.e., arrangement of vessel-ray pitting (Fig. 7), the type of vessel-ray pitting (Fig. 8), the shape of body ray cells in multiseriate rays (Fig. 9), and the presence of secretory ducts (Fig. 10). These features are chosen based on their apparent consistency within the various subclades of Vaccinieae and on previous studies within the family (Lens et al., 2003, 2004a).

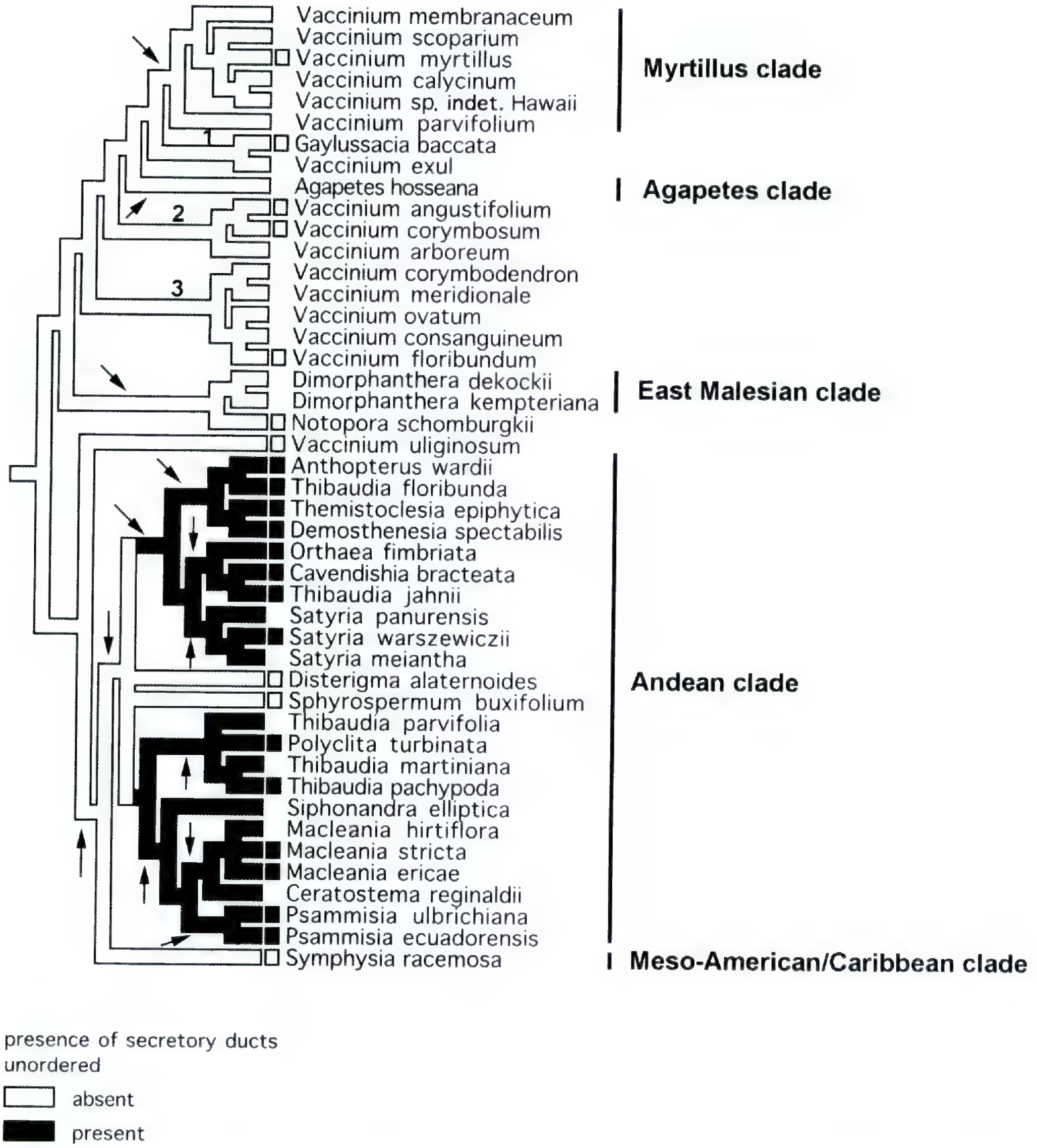

Figure 10. Modified tree based on the molecular analyses of Kron et al. (2002b) and Powell and Kron (2002, 2003) showing the presence of secretory ducts in the primary xylem and the pith of Vaccinieae. Clades one, two, and three represent an intermediate group based on their wood structure. Arrows indicate bootstrap values of at least 85%. Missing blocks indicate that the pith and primary xylem tissue was not available.

Myrtillus Clade (represented by Vaccinium calycinum, V. membranaceum, V. myrtillus, V. parvifolium, V. scoparium, *and* V. *sp. indet. Hawaii)*

The enlarged Myrtillus clade sensu Powell and Kron (2002) mostly occurs along the Pacific Rim from Japan to Mexico (Powell & Kron, 2002). The species studied are wood anatomically defined by the presence of exclusively or mainly scalariform perforations, opposite to scalariform vessel-ray pitting with distinctly bordered pits (Figs. 7, 8), and narrow (2- to 5-seriate) and low multiseriate rays (often lower than 1000 μm) with mainly procumbent body ray cells (Fig. 9). It is remarkable that this set of characters is common in non-vaccinioid Ericaceae (see also Cox, 1948; Suzuki & Noshiro, 1988).

Agapetes Clade (represented by Agapetes hosseana *only)*

This clade contains temperate and tropical Asian *Vaccinium* species and species of *Agapetes* (Kron et

al., 2002b). Although we have studied several *Agapetes* species, only *A. hosseana* is included in the molecular tree. This species shows some features that resemble the Myrtillus clade, for instance, the presence of distinctly bordered vessel-ray pitting (Fig. 8), and the relatively narrow and low multiseriate rays. On the other hand, other *Agapetes* species investigated are characterized by very broad (3- to 15-seriate) and high multiseriate rays (sometimes more than 10,000 μm in *A. sikkimensis* and *A. moorei*). The only characters that seem to distinguish this group from the Myrtillus clade are (1) the presence of alternate vessel-ray pitting, which is also seen outside the Agapetes clade in a few *Vaccinium* species and in many non-vaccinioid Ericaceae, and (2) the occurrence of procumbent, square and upright body ray cells in the multiseriate rays, although this type of ray composition is also seen in *Vaccinium membranaceum* (Figs. 7, 9).

East Malesian Clade (represented by Dimorphanthera dekockii *and* D. kempteriana*)*

The East Malesian clade comprises species belonging to *Dimorphanthera* and *Paphia* (Kron et al., 2002b). The two *Dimorphanthera* species that are used in this study differ from the Agapetes and Myrtillus clades by the presence of wide vessel elements (ranging from 60 μm to 205 μm) with almost exclusively simple perforation plates, mainly scalariform vessel-ray pits with strongly reduced borders (Figs. 7, 8), and the occurrence of prismatic crystals in multiseriate rays. Furthermore, the two species studied are also defined by an abundant presence of tracheids and a small amount of fiber-tracheids, and broad (4- to 11-seriate) and high multiseriate rays (1800–8400 μm). The high percentage of wide vessels with simple perforations and the abundant occurrence of tracheids is likely due to the climbing habit of *Dimorphanthera* (see also Lens et al., 2004b).

Meso-American/Caribbean Clade (represented by Symphysia racemosa *only)*

This is a well-supported clade that contains species generally found in Central America and the Caribbean (Kron et al., 2002b). The species examined in this study shows mainly scalariform vessel perforations, exclusively scalariform vessel-ray pits with strongly reduced borders, and relatively narrow multiseriate rays (4-seriate) with procumbent, square and upright body ray cells (Figs. 7–9). It is worth mentioning that similar vessel-ray pits are found in the East Malesian clade and the Andean clade.

Andean Clade (represented by Anthopterus wardii, Cavendishia bracteata, Ceratostema reginaldii, Demosthenesia spectabilis, Disterigma alaternoides, Macleania ericae, M. hirtiflora, M. stricta, Orthaea fimbriata, Polyclita turbinata, Psammisia ecuadorensis, P. *cf.* ulbrichiana, Satyria meiantha, S. panurensis, S. warszewiczii, Siphonandra elliptica, Sphyrospermum buxifolium, Themistoclesia epiphytica, Thibaudia floribunda, T. jahnii, T. parvifolia, T. pachypoda, *and* T. martiniana*)*

The Andean clade shows by far the highest species diversity within Vaccinieae, and is concentrated in the moist, montane forests of the northern Andes. This group has evolved very recently, about 20 million years ago when the Andes began to rise (Luteyn, 2002). This can also be illustrated by its homogeneous wood structure. Species of the Andean clade are characterized by scalariform vessel-ray pits with strongly reduced borders (Figs. 7, 8), and by broad (4- to 14-seriate) and high (often more than 3000 μm) multiseriate rays with a high percentage of square and upright body ray cells (Fig. 9). Furthermore, prismatic crystals often occur in ray cells as well as in axial parenchyma cells. The most distinguishing character, however, is the occurrence of secretory ducts near the primary xylem and the pith tissue. All specimens with secretory ducts are included in the Andean clade (Table 1), but this character is sometimes lacking in, for instance, the two unplaced species, i.e., *Disterigma alaternoides* and *Sphyrospermum buxifolium* (Fig. 10).

Within the Andean clade, wood anatomical support for the division into the two major subclades is lacking. Nevertheless, the sister relationship of the Andean clade with the Meso-American/Caribbean clade seems justified according to wood anatomical data: both clades show mainly scalariform vessel perforations, scalariform vessel-ray pits with strongly reduced borders, and distinctly upright body ray cells (Figs. 7–9).

Remaining Subclades (represented by Gaylussacia baccata, Notopora schomburgkii, Vaccinium angustifolium, V. arboreum, V. consanguineum, V. corymbodendron, V. corymbosum, V. exul, V. floribundum, V. meridionale, V. ovatum, *and* V. uliginosum*)*

Because the monophyly and the taxonomic position of the remaining subclades is still debatable, it is difficult to speculate on the wood anatomical trends in these groups. Wood anatomically, it seems that clades one to three, comprising several *Vaccinium* species and *Gaylussacia baccata* (Figs. 7–10, clades 1–3), form an intermediate group between

the Myrtillus clade and the group including the East Malesian clade, the Meso-American/Caribbean clade and the Andean clade. Wood features that illustrate the intermediate position of clades one to three include the presence of (1) minutely bordered pits in *Gaylussacia baccata*, *Vaccinium corymbodendron*, *V. consanguineum*, and *V. ovatum* (Fig. 8), (2) prismatic crystals in ray cells of *V. corymbosum*, *V. meridionale*, and *V. ovatum*, and (3) relatively broad (6–12-seriate in *V. exul*) and high multiseriate rays in some species (up to 4200 μm in *V. corymbosum*). The taxonomic position of *Vaccinium uliginosum*, which is placed as sister to the Andean clade and the Meso-American/Caribbean clade, is not supported wood anatomically because none of the above-mentioned intermediate characters are present.

The taxonomic position of *Notopora schomburgkii* as sister to the East Malesian clade is wood anatomically supported by the occurrence of simple vessel perforations, scalariform vessel-ray pits with strongly reduced borders (Figs. 7, 8), and the occurrence of prismatic crystals in the rays. Furthermore, the same features are also present in some representatives of the Andean clade, as in, for instance, *Satyria meiantha*, *S. panurensis*, *Thibaudia floribunda*, and *T. pachypoda*.

The possible relationship of *Dimorphanthera* and *Satyria* as suggested by Stevens (1974) is wood anatomically disputable: the two genera share several similar wood features, like scalariform vessel ray-pits with much reduced borders, high multiseriate rays and prismatic crystals in ray cells, but these features are very common in the Andean clade. In addition, the two genera show a high percentage of simple vessel perforations in their wood, a feature that is relatively rare in the Andean clade, but this is probably due to the climbing habit of *Dimorphanthera* and *Satyria*.

Structure of Multiseriate Rays

The taxonomic value of multiseriate rays with mainly square and upright body ray cells in Vaccinieae is somewhat unexpected in a family containing many shrubs with relatively thin stems. It is known that upright body ray cells are abundantly present near the pith while more procumbent cell shapes are found closer to the cambium. Indeed, the mean stem diameter of the *Vaccinium* species studied is larger than the stem diameter of the Andean clade species. This could explain the presence of exclusively procumbent body ray cells in *Vaccinium* in regard to the mainly square to upright body ray cells in the wood of the Andean clade species. However, thick wood samples of the Andean clade (e.g., *Ceratostema reginaldii*, *Satyria meiantha*, and *S. panurensis*) and the East Malesian clade (*Dimorphanthera kempteriana*) also show many upright and square body ray cells. Moreover, only mature stems of species belonging to the Andean clade were collected during various field trips. This indicates that the shape of body ray cells contains a phylogenetic signal within Vaccinioideae, as mentioned by Lens et al. (2004a).

Wood Anatomical Comparison with Other Ericaceae s.l.

The wood structure of Vaccinieae shows many similarities with that of Ericaceae s.l. Examples include the diffuse-porosity, narrow and solitary vessels with an angular vessel outline, high vessel frequency, scalariform and/or simple vessel perforations, tracheids, distinctly bordered fiber pits (fiber-tracheids), scarcely distributed axial parenchyma, and the combination of uniseriate rays with less common multiseriate rays. The study group corresponds especially to other tribes of the subfamily Vaccinioideae as well as to the related epacrids (subfamily Styphelioideae). As mentioned by Lens et al. (2003, 2004a), the presence of wide and high multiseriate rays, which are nearly absent outside Styphelioideae and Vaccinioideae, may support the relationship between both subfamilies. In addition, the sporadic occurrence of libriform fibers and the presence of crystal-bearing axial parenchyma cells are found in both subfamilies, but these two features also occur in the distantly related subfamily Arbutoideae (Lens, pers. obs.).

Most genera of Vaccinieae, except for the large genus *Vaccinium*, can easily be distinguished from other Ericaceae by a set of wood anatomical features. These features include the presence of scalariform vessel-ray pits with strongly reduced borders, high multiseriate rays (often more than 3000 μm) with mainly square to upright body ray cells containing prismatic crystals, and the occurrence of undivided axial parenchyma cells, which usually range from 500 to 900 μm.

Conclusions

The wood structure of the tribe Vaccinieae, considered to be a derived tribe within the Ericaceae, fits well within the family and shows some taxonomically important characters. Many species of *Vaccinium* show several wood features that correspond with a typical Ericaceae wood sample: distinctly bordered vessel-ray pits, and narrow (2- to 4-seriate) and low (often less than 1000 μm) mul-

tiseriate rays, which mainly consist of procumbent body ray cells. Other clades within Vaccinieae, represented by the East Malesian clade, the Meso-American/Caribbean clade, and the Andean clade, show a set of characters that are absent in other members of the family, viz. scalariform vessel-ray pits with strongly reduced borders, a high portion of upright body ray cells (although exclusively procumbent in *Dimorphanthera kempteriana*), wide (4- to 14-seriate) and high multiseriate rays (often more than 3000 μm), and prismatic crystals in chambered ray cells (but absent in *Symphysia racemosa*). Furthermore, the presence of secretory ducts in the primary xylem and in the pith, which is frequently observed in the Andean clade, seems to represent a feature otherwise lacking in the family. In addition, the presence of long, non-divided axial parenchyma cells in most species of Vaccinieae distinguishes this tribe from the rest of the subfamily.

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Index to Specimens Examined

The wood samples studied are listed below with reference to the origin, collector, and the diameter of the wood sample in mm. "Mature" means that the wood sample is derived from a mature branch, although the exact diameter could not be traced. Authors of plant names are according to Brummit and Powell (1992). Two samples were preserved in FAA to investigate living substances in fibers. Institutional wood collections used in this study are abbreviated according to the *Index Xylariorum* (Stern, 1988). Other institutions that were used to collect wood samples are The National Botanic Garden of Belgium (BR), The Royal Botanic Gardens, Edinburgh (E), and The New York Botanical Garden (NY).

Agapetes flava (Hook. f.) Sleumer: BHUTAN. **Chukka,** *A. Grierson & D. Long 3076* (E 19822403), 10 mm; *A. hosseana* Diels: THAILAND. **Chiang Mai,** *B. L. Burtt 958* (E 19672592), 7 mm; *A. mannii* Hemsl.: MYANMAR. *F. Kingdon-Ward 19097* (E 19500046), 10 mm; *A. moorei* Hemsl.: origin and collector unknown (E 19696069), 10 mm; *A. sikkimensis* Airy Shaw: BHUTAN. **Phuntsholing,** *I. Sinclair & D. Long 5778* (E 19842032), 12 mm; *A. variegata* G. Don: INDIA. **Meghalaya,** *D. F. Chamberlain 106* (E 19751313), 9 mm.

Anthopterus wardii Ball: COLOMBIA. **Nariño,** *J. L. Luteyn & M. Lebrón-Luteyn 6865* (NY), 8 mm; *A. wardii* Ball: COLOMBIA. *van Rooden et al. 443* (Uw 25586), 7 mm.

Cavendishia bracteata (J. St.-Hil.) Hoerold: BOLIVIA. **La Paz,** *L. J. Dorr et al. 6890* (Lw), 12 mm; *C. compacta* A. C. Sm.: COLOMBIA. *van Rooden et al. 555* (Uw 25619), 15 mm; *C. callista* Donn. Sm.: SURINAM. **Lely Mountains,** *Lindeman & Stoffers 502* (Uw 21835), 11 mm; *C. lindauiana* Hoerold: COLOMBIA. *van Rooden et al. 630* (Uw 25642), 15 mm; *C. pubescens* (Kunth) Hemsl.: VENEZUELA. *L. Williams 10020* (Uw 35101), 43 mm; *C. urophylla* A. C. Sm.: COLOMBIA. *van Rooden et al. 371* (Uw 25568), 21 mm.

Ceratostema reginaldii (Sleumer) A. C. Sm.: ECUADOR. **Loja,** *G. P. Lewis 3345* (Kw 74944), 20 mm; *C. reginaldii* (Sleumer) A. C. Sm.: ECUADOR. **Loja,** *L. J. Dorr & I. Valdespino 6562* (Lw), 15 mm.

Demosthenesia spectabilis (Rusby) A. C. Sm.: PERU. **Cuzco,** *J. L. Luteyn 6452* (NY), 7 mm.

Dimorphanthera collinsii Sleumer var. *collinsii*: INDONESIA. **Irian,** *Kalkman 4902* (Tw 23696), 60 mm; *D. cornuta* J. J. Sm. var. *cornuta*: EAST NEW GUINEA. *Vink 17084* (Kw 11639, Uw 18298), 51 mm; *D. dekockii* J. J. Sm. var. *pubiflora* Sleumer: EAST NEW GUINEA. *Vink 17307* (Kw 11639, Uw 18316), 45 mm; *D. kempteriana* Schltr.: INDONESIA. **East Irian,** *Vink 16888* (Tw 23733), 44 mm.

Diogenesia floribunda (A. C. Sm.) Sleumer: ECUADOR. **Napo-Pastaza,** *J. L. Luteyn & M. Lebrón-Luteyn 5675* (NY), 9 mm; *D. tetrandra* (A. C. Sm.) Sleumer: COLOMBIA. **Cauca,** *J. L. Luteyn et al. 7388* (NY), 11 mm.

Disterigma sp. indet.: PERU. **Loreto,** collector unknown (Tw 31380), 10 mm; *D.* sp. indet.: PERU. **Cajamarca,** *C. Carton 54* (BR), 8 mm; *D. alaternoides* Nied.: COLOMBIA. **Cauca,** *J. L. Luteyn et al. 7400* (NY), 11 mm; *D. cryptocalyx* A. C. Sm.: COLOMBIA. **Huila,** *J. L. Luteyn & M. Lebrón-Luteyn 7545* (NY), 7 mm.

Gaylussacia baccata K. Koch (preserved in FAA): BELGIUM. *F. Lens* (BR), 7 mm; *G. decipiens* Cham. var. *decipiens*: BRAZIL. *P. Clausen 1840* (BR), 6 mm.

Lateropora ovata A. C. Sm.: PANAMA. **Chiriquí,** *J. L. Luteyn 15294* (NY), 9 mm.

Macleania crassa A. C. Sm.: COLOMBIA. **Cauca,** *J. L. Luteyn et al. 7378* (NY), 20 mm; *M. ericae* Sleumer: ECUADOR. **Pichincha,** *J. L. Luteyn & M. Lebrón-Luteyn 5639* (NY), 15 mm; *M. hirtiflora* (Benth.) A. C. Sm.: COLOMBIA. **Cauca,** *J. L. Luteyn et al. 7386* (NY), 13 mm; *M. loeseneriana* Hoerold: ECUADOR. **Carchi,** *J. L. Luteyn & M. Lebrón-Luteyn 5726* (NY), 18 mm; *M. pentaptera* Hoerold: COLOMBIA. **Valle,** *J. L. Luteyn & M. Lebrón-Luteyn 6957* (NY), 19 mm; *M. rupestris* (Kunth) A. C. Sm.: VENEZUELA. *L. Williams 10904* (Uw 35316), 18 mm; *M. stricta* A. C. Sm.: ECUADOR. **Carchi,** *J. L. Luteyn & M. Lebrón-Luteyn 5744* (NY), 10 mm.

Mycerinus chimantensis Maguire, Steyerm. & Luteyn: VENEZUELA. **Bolívar,** *O. Huber 9010* (NY), 7 mm.

Notopora cardonae A. C. Sm.: VENEZUELA. **Bolívar,** *J. L. Luteyn 9596* (NY), 10 mm; *N. schomburgkii* Hook. f.: VENEZUELA. *Maas et al. 5808* (Uw 27397), 10 mm.

Oreanthes ecuadorensis Luteyn: ECUADOR. **Loja,** *J. L. Luteyn 15394* (NY), 4 mm.

Orthaea fimbriata Luteyn: ECUADOR. **Morona-Santiago,** *J. L. Luteyn & M. Lebrón-Luteyn 5794* (NY), 15 mm.

Plutarchia ecuadorensis Luteyn: ECUADOR. **Azuay,** *J. L. Luteyn & M. Lebrón-Luteyn 5778* (NY), 13 mm; *P. rigida* (Benth.) A. C. Sm.: COLOMBIA. **Cauca,** *J. L. Luteyn 10108* (NY), 5 mm.

Polyclita turbinata (Kuntze) A. C. Sm.: BOLIVIA. **Cochabamba,** *J. L. Luteyn 15453* (NY), 10 mm.

Psammisia sp. indet.: COLOMBIA. *van Rooden et al. 359* (Uw 25565), 30 mm; *P. ecuadorensis* Hoerold: ECUADOR. **Pichincha,** *J. L. Luteyn & M. Lebrón-Luteyn 5621* (NY), 7 mm; *P. ferruginea* A. C. Sm.: ECUADOR. *Maas et al. 3041* (Uw 23589), 20 mm; *P. graebneriana* Hoerold: COLOMBIA. **Nariño,** *J. L. Luteyn & M. Lebrón-Luteyn 6809* (NY), 10 mm; *P. guianensis* Klotzsch: VENEZUELA. **Amazonas,** *B. Maguire et al. 42397* (Tw 36530), 11 mm; *P. guianensis* Klotzsch: ECUADOR. **Azuay,** *Camp 4367* (Uw 10655), 11 mm; *P. penduliflora* (Dunal) Klotzsch: VENEZUELA. **Trujillo,** *J. L. Luteyn et al. 5223* (NY), 8 mm; *P.* cf. *ulbrichiana* Hoerold: ECUADOR. **Pichincha,** *J. L. Luteyn & M. Lebrón-Luteyn 6532* (NY), 12 mm.

Satyria sp. indet.: COLOMBIA. **Antioquia,** *J. L. Luteyn et al. 7017* (NY), 16 mm; *S.* sp. indet.: BRAZIL. *B. Maguire et al. 48650* (Uw 16976), 35 mm; *S.* sp.

indet.: BRAZIL. *B. Maguire et al. 46784* (Uw 17005), 22 mm; *S.* sp. indet.: COLOMBIA. **Antioquia,** *J. L. Luteyn & M. Lebrón-Luteyn 7177* (NY), 15 mm; *S. carnosiflora* Lanj.: VENEZUELA. **Amazonas,** *B. Maguire et al. 42061* (Tw 36580), 15 mm; *S. meiantha* Donn. Sm.: MEXICO. *D. Breedlove 9746* (MADw 23933), mature; *S. panurensis* (Meisn.) Nied.: BRAZIL. *B. Maguire et al. 48650* (MADw 20301), mature; *S. warszewiczii* Klotzsch: MEXICO. **Veracruz,** *R. T. Cedillo & J. I. Calzada 170* (BR), 10 mm; *S. warszewiczii* Klotzsch: origin unknown, *Warszewicz,* (BR), 12 mm.

Semiramisia pulcherrima A. C. Sm.: COLOMBIA. **Nariño,** *J. L. Luteyn 15210* (NY), 9 mm.

Siphonandra elliptica Klotzsch: PERU . **Cuzco,** *J. L. Luteyn & M. Lebrón-Luteyn 6377* (NY), 14 mm.

Sphyrospermum sp. indet.: ECUADOR. **Pichincha,** *G. Argent* (E 19762390), 11 mm; *S. buxifolium* Poepp. & Endl.: ECUADOR. *G. Argent* (E 19762390), 6 mm; *S. sodiroi* A. C. Sm.: ECUADOR. **Pichincha,** *G. Argent 526* (E 19762398), 6 mm.

Symphysia racemosa (Vahl) Stearn: DOMINICA. *Chambers 2555* (Uw 15385), 22 mm.

Themistoclesia epiphytica A. C. Sm.: COLOMBIA. *A. M. Cleef 2652* (Uw 20767), 5 mm; *T. pendula* Klotsch: VENEZUELA. **La Mucuy,** *Breteler 3476* (Uw 11013), 35 mm; *T. vegasana* A. C. Sm.: COLOMBIA. **Boyacá,** *J. L. Luteyn et al. 7590* (NY), 13 mm.

Thibaudia angustifolia Hook.: PERU. **Amazonas,** *J. L. Luteyn & M. Lebrón-Luteyn 5528* (NY), 13 mm; *T. floribunda* HBK: ECUADOR. **Carchi,** *J. L. Luteyn & M. Lebrón-Luteyn 5725* (NY), 14 mm; *T. formosa* (Klotzsch) Hoerold: VENEZUELA. **Amazonas,** *B. Maguire et al. 27673* (Tw 36552), 20 mm; *T. jahnii* S. F. Blake: VENEZUELA. **Mérida,** *J. L. Luteyn et al. 6185* (NY), 15 mm; *T. martiniana* A. C. Sm.: ECUADOR. **Pichincha,** *J. L. Luteyn & M. Lebrón-Luteyn 5654* (NY), 24 mm; *T. pachypoda* A. C. Sm.: COLOMBIA. *Cuatrecasas 19876* (Uw 25099), 11 mm; *T. parvifolia* Hoerold: COLOMBIA. **Cauca,** *J. L. Luteyn & M. Lebrón-Luteyn 6897* (NY), 14 mm; *T. rigidiflora* A. C. Sm: COLOMBIA. **Valle,** *J. L. Luteyn & M. Lebrón-Luteyn 6985* (NY), 23 mm.

Vaccinium sp. indet.: U.S.A. **Hawaii,** *W. Stern 2980* (Tw 24148), 33 mm; *V. africanum* Britton: AFRICA. *H. Brown 52* (Kw 11707), 70 mm; *V. angustifolium* Benth. (preserved in FAA): BELGIUM. *E. Lens* (BR), 6 mm; *V. arboreum* Marshall: U.S.A. **Texas,** *H. Nogle 258* (Tw 18270), mature; *V. atrococcum* A. Heller: U.S.A. **Maryland,** collector unknown (Kw 11706), mature; *V. bancanum* Miq.: BRUNEI. Collector unknown, (Kw 74737), 67 mm; *V. barandanum* Vidal var. *barandanum*: PHILIPPINES. *M. Jacobs 7249* (Uw 33743), 45 mm; *V. berberidifolium* (A. Gray) Skottsb.: U.S.A. **Hawaii,** *Stern & Herbst 496* (Uw 18579), 9 mm; *V. bracteatum* Thunb.: CHINA. **Guangdong,** *Forest Research Institute 1623* (Tw 42071), mature; *V. calycinum* Sm.: U.S.A. **Hawaii,** *W. Stern 2950* (Tw 24121), 17 mm; *V. consanguineum* Klotzsch: COSTA RICA. **San José,** *M. Wiemann 13* (Uw 30897), mature; *V. corymbodendron* Dun.: COLOMBIA. *J. Cuatrecasas 20784* (Tw 20784), mature; *V. corymbosum* L.: CANADA. **Québec,** *R. Dechamps 5003* (Tw 33895), 8 mm; *V. cumingianum* Vidal: PHILIPPINES. *M. Jacobs 7270* (Uw 33746), 36 mm; *V. exaristatum* Kurz: INDIA. **Assam,** Lushai Hills, *N. E. Parry 45* (Kw 11747), 36 mm; *V. exul* Bolus: SOUTH AFRICA. *J. Prior 464,* 23 mm; *V. floccosum* (L. O. Williams) Wilbur & Luteyn: PANAMA. **Chiriquí.** *Maas et al. 4957* (Uw 26277), 33 mm; *V. floribundum* HBK: BOLIVIA. **Cumba de Sama,** *J. R. De Sloover 399* (BR), 5 mm; *V. globulare* Rydb.: U.S.A. **Washington,** *R. Dechamps 4460* (Tw 46335), 15 mm; *V. leschenaultii* Wight: INDIA. Collector unknown (Kw 70598), mature; *V. leucanthum* Schltdl.: MEXICO. **Puebla,** *L. Lebacq 73* (Tw 24590), adult; *V. maderense* Link: SPAIN. **Madeira,** *N. H. Mason* (Kw 11745), mature; *V. membranaceum* Hook.: U.S.A. **Oregon,** *R. Dechamps 4325* (Tw 46029), 9 mm; *V. meridionale* Sw.: VENEZUELA. *L. Williams 10896* (Uw 35314), mature; *V. myrtillus* L.: BELGIUM. **Luik,** *R. Dechamps* (Tw 43142), 8 mm; *V. occidentale* A. Gray: U.S.A. **Oregon,** *R. Dechamps 4414* (Tw 46260), mature; *V. ovatum* Pursh: U.S.A. **Oregon,** *R. Dechamps 4418* (Tw 46267), 23 mm; *V. parvifolium* Sm.: U.S.A. **Oregon,** *R. Dechamps 4310* (Tw 45996), 27 mm; *V. puberulum* C. F. W. Meissn. var. *subcrenulatum* Maguire, Steyerm. & Luteyn: GUYANA. *Maas et al. 5733* (Uw 27342), 13 mm; *V. scoparium* Leiberg: U.S.A. **Oregon,** *R. Dechamps 4383* (Tw 46187), 6 mm; *V. stanleyi* Schweinf.: DEMOCRATIC REPUBLIC OF CONGO. **Kivu,** P. Deuse 55 (BR), 9 mm; *V. uliginosum* L: NORWAY. **Hordaland,** *R. Dechamps 6033* (Tw 38581), 6 mm.

REVISION OF *DRACONTIUM* (ARACEAE)[1]

Guanghua Zhu[2] *and Thomas B. Croat*[2]

Abstract

A taxonomic revision of the genus *Dracontium* L. (Araceae) is presented predominantly from morphological, anatomical, and phytogeographic data. *Dracontium* is treated as comprising 23 species, including 10 new species: *D. amazonense* G. Zhu & Croat, *D. angustispathum* G. Zhu & Croat, *D. asperispathum* G. Zhu & Croat, *D. bogneri* G. Zhu & Croat, *D. grandispathum* G. Zhu & Croat, *D. grayumianum* G. Zhu & Croat, *D. guianense* G. Zhu & Croat, *D. peruvianum* G. Zhu & Croat, *D. ploemanii* G. Zhu & Croat, and *D. prancei* G. Zhu & Croat. Five names are newly lectotypified herein: *Amorphophallus nivosus* Lem., *A. papillosus* hort. ex Rafarin, *Dracontium elatum* Masters, *D. pittieri* Engl., and *D. soconuscum* Matuda. The following species are newly synonymized: *D. carderi* Hook. f., *D. costaricense* Engl., *D. dressleri* Croat, *D. lineare* G. S. Bunting & Tillett, *D. loretense* K. Krause, *D. ornatum* K. Krause, *D. trianae* Engl., and *Echidnium regelianum* Engl. All taxa are described and illustrated.

Key words: Araceae, *Dracontium*, monograph, taxonomy.

The Araceae are a family of herbaceous monocots with 106 genera and approximately 3500 species, the vast majority occurring in the New World tropics (Croat, 1988, 1992). The *World Checklist and Bibliography of Araceae (and Acoraceae)* lists a total of 2824 recorded species (Govaerts & Frodin, 2002). Members of the family are highly diverse in life form, leaf morphology, and inflorescence characteristics. Life forms range from submerged or free-floating aquatics to terrestrial (sometimes tuberous), epiphytic or hemiepiphytic plants, to climbers. Leaves range from simple and entire to compound and highly divided, and may be basal or produced from an aerial stem. The family is best characterized by its distinctive inflorescence, a spadix with bisexual or unisexual flowers (sometimes with a sterile region) subtended by a solitary pedunculate spathe.

The present study of *Dracontium* L. comprises a taxonomic revision of one of the most poorly known tuberous genera in the Araceae. *Dracontium*, as here recognized with 23 species, represents the most species-rich tuberous genus of the Araceae in the New World. Vegetatively, it shares a great similarity with the Old World genus *Amorphophallus* Blume ex Decne. Plants in both genera usually consist of a single leaf arising from an underground tuber with a more or less mottled, reptilian-patterned petiole up to several meters long with a highly divided, compound, spreading blade reaching as much as three meters or more in diameter. Inflorescences of both genera are notorious for their fetid scents at anthesis. However, *Dracontium* differs sharply from *Amorphophallus* in having bisexual flowers on a uniform spadix.

Accurate identification of *Dracontium* species has been difficult because of the paucity and inadequacy of herbarium material and their sporadic phenology. Herbarium specimens, though comparatively abundant for some species such as *Dracontium spruceanum* (Schott) G. Zhu, are frequently sterile and often incomplete since mature adult leaves are almost always too large to be mounted on a single herbarium sheet. Frequently, a single leaf is mounted on several to many herbarium sheets. Hence, intensive study of living material in the field or under cultivation is essential. Though local populations may contain many plants, populations of *Dracontium* are often widely scattered and single individuals not frequently encountered. Under unfavorable growing conditions, plants of *Dracontium* may remain vegetative for many years,

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and often go dormant for two to four months in the dry season. Inflorescences of *Dracontium* often arise from the apex of the tuber before or after leaf development. Therefore, matching fertile with sterile herbarium material of the same *Dracontium* species is often problematic.

Live plants of *Dracontium* are not uncommon in cultivation in botanical gardens and aroid nurseries, as they share an ornamental appeal with *Amorphophallus* species and are easy to propagate and maintain. Unfortunately, cultivated material of *Dracontium* is limited to only a few species, such as *D. gigas* (Seem.) Engl., *D. polyphyllum* L., and *D. spruceanum*. Locating these plants in the field is often not difficult since populations of *Dracontium* are usually well known to native people due to the distinctive, reptilian-patterned petioles and medicinal uses.

Materials and Methods

This revision was conducted mainly at the Missouri Botanical Garden, where the largest living and herbarium collections of *Dracontium* in the world are housed. Field research for this study was conducted in Costa Rica, Panama, and Brazil between 1992 and 1995. Trips were made to several botanical gardens to study cultivated plants, including the Marie Selby Botanical Gardens and The New York Botanical Garden in the Unites States, and the São Paulo Botanical Garden and Botanical Garden of Rio de Janeiro in Brazil, as well as to herbaria CR, F, GH, HB, IAN, IBGE, ISC, MG, NY, PMA, R, RB, SCZ, SEL, SP, SPSF, UB, UEC, US, and WSU. Over 670 collections comprising about 3000 herbarium sheets, including loans from 49 major institutions worldwide, were studied (see Appendices 1, 2). Data from all cited specimens are recorded in the Missouri Botanical Garden database TROPICOS.

In this study, we have relied heavily upon live collections, especially the second author's gatherings during his more than 35 years of fieldwork in the Neotropics. Some species, such as *Dracontium guianense* G. Zhu & Croat, are known only from a few herbarium collections. In such cases, descriptions are from herbarium specimens only. Due to the rarity of many *Dracontium* species, all specimens with proper collecting information are cited, including those prepared from cultivated plants. For species determinations, we have also relied on photographs prepared by Croat and many other individuals to reconstruct the natural habits for these plants.

Descriptions of species were prepared using the DELTA (DEscriptive Language for TAxonomy) program (Dallwitz et al., 1995). The program TAXASOFT (Gouda, 1994) was used for data maintenance of DELTA. The exsiccatal information was prepared by using TROPICOS. Ecological zones are estimated by using the Holdridge Life Zone system (Holdridge et al., 1971).

Material for chromosomal studies was obtained from plants cultivated at the Missouri Botanical Garden. Growing root tips were treated in 0.002M 8-hydroxyquinoline for 4 hr. before being fixed in ethanol-glacial acetic acid-chloroform (6:3:1) at 8°C overnight. Root tips were then rotated through a hydrated 70%–50%–25%–10% ethanol series, were macerated with 1N HCl (room temperature) for 10 minutes, 1N HCl (60°C) for 8 min., and 1N HCl (room temperature) for another 10 min., and rinsed with deionized H_2O for 30 min. before being stained in 0.5% Feulgen for 1.5 hr. (Masahiro Takei, pers. comm.). Finally, the plant material was rinsed with deionized water, and slides with the chromosome squashes were prepared.

Taxonomic History

The first mention of a species referable to *Dracontium* appeared in Hermann's *Paradisi batavi prodromus* (1689: 315) as "*Arum polyphyllum, dictum Dracontium, caule scabro punicante, surinamense*" and "*Dracontium americanum caule scabro puniceo radice Cyclaminis.*" The plant was introduced into the gardens of Holland by the early Dutch plant-hunters from Surinam in the second half of the 17th century. A corresponding plate was later published by Plukenet (1696, t. 149, fig. 1) in his *Almagestum* under the name "*Arum polyphyllum surinamense caule atrorubente glabro et eleganter variegato.*" This same species was redescribed by Hermann (1698: 93–94) in his *Paradisus batavus* as "*Dracontium americanum scabro puniceo caule radice Cyclaminis,*" along with a figure (t. 93) under the name "*Arum polyphyllum caule scabro punicante.*" Linnaeus (1737) published the first comprehensive description of this species after he personally studied a flowering specimen in the Clifford Garden at Hartecamp, Holland. Later, he validly published the genus *Dracontium* with five species in *Species Plantarum* and established the binominal *Dracontium polyphyllum* (Linnaeus, 1753), which is the only species still recognized within *Dracontium*. Under *D. polyphyllum*, Linnaeus (1753: 967) cited both Plukenet's and Hermann's figures. Hermann's figure was later selected as the lectotype of *D. polyphyllum* (Hay, 1992). Since *D. polyphyllum* was referred to as "typical" by Britton and Wilson (1923: 130), it was accepted

as the generic type of *Dracontium* (Jarvis et al., 1993: 43).

Rafinesque (1838: 12–13) evidently misidentified a plant as *D. polyphyllum* saying "the scandent sp. appear the type of *Dracontium*, which Anderson changed to Mostera perhaps a better name," and superfluously renamed *D. polyphyllum* as *Eutereia nigricans* Rafinesque. Therefore, the generic name *Eutereia* is a superfluous name for *Dracontium*.

The genus *Dracontium* remained known only with one species from Surinam until Richard Schomburgk's expedition to Guyana (1840–1844), during which he collected a second species of the genus. Several living tubers of this species were sent to the Botanical Garden of Berlin, Germany, in 1843 (Roth, 1922, 1923; Zhu et al., 1998). This species was later described by Kunth (1844) as *D. dubium* Kunth. Schott (1857b) transferred this species to his newly described genus *Echidnium* Schott and created a superfluous name, *E. schomburgkii* Schott (Zhu et al., 1998). According to Schott (1857b), *Echidnium* is ostensibly distinguished from *Dracontium* by having a unilocular ovary with two ovules, as opposed to a bi- or pluri-locular ovary in *Dracontium*.

When describing the single species in his new genus *Ophione* Schott, Schott (1857a) described a third species of *Dracontium* as *O. purdieana* Schott, which differs from *Echidnium* in having an ovary with 4 to 5 locules, and from *Dracontium* in having a long-acuminate spathe. Later, Schott (1858a) described another *Dracontium* species as *Echidnium spruceanum* Schott before publishing the first comprehensive classification of the Araceae in the *Prodromus systematis aroidearum* in 1860, which laid the foundation for the modern generic concepts within the aroid family. In his *Prodromus* (1860), Schott recognized four *Dracontium* species in three genera, namely *Dracontium*, *Echidnium*, and *Ophione*, classified along with *Symplocarpus* Salisbury in Araceae subtribe Dracontiinae next to subtribe Lasiinae in the tribe Orontieae: *Dracontium polyphyllum*, *Echidnium schomburgkii*, *E. spruceanum*, and *Ophione purdieana*. The superfluous name *E. schomburgkii* was used for *D. dubium* (Zhu et al., 1998). The diagnostic features used by Schott (1860) for his separation of these genera were based exclusively on floral characters such as spathe and spadix shapes, tepal number and shape, stigma lobes, ovary number and shape, and number of ovules per locule. All these characters may be useful for the separation of species within the group, but not for defining generic boundaries.

Unable to confirm the characters of unilocular ovary with two ovules for *Echidnium* and the importance of the floral characters, Engler (1889) transferred *Echidnium* as a section to *Dracontium* while recognizing *Ophione*, but later revived the generic status of *Echidnium* in his *Das Pflanzenreich* (1911) and synonymized *Ophione* within *Dracontium*. Bogner (1985) and Hay (1988) noted that a unilocular ovary with two ovules cannot be used as a generic character in this group and once again synonymized *Echidnium* within *Dracontium*. The supposedly unilocular ovary with two ovules of *E. dubium* (Kunth) Engl. is erroneous based on its neotype (Zhu et al., 1998), as well as the type of *E. spruceanum* (Zhu, 1996). Unilocular ovaries do not occur in *Dracontium* and this genus never has more than one ovule in each locule: these stand as generic traits of the genus (Zhu, 1995, 1996; Zhu et al., 1998). *Echidnium spruceanum* Schott was recently transferred to *Dracontium* by Zhu (1996).

Koch (1859) described a fifth species, *D. asperum* K. Koch, from a plant cultivated at the Berlin Botanical Garden. This plant had been obtained from the Botanical Garden in Amsterdam and originated from Surinam (Koch, 1859). This species was apparently unknown to Schott in 1860. Because of the same country of origin and the ambiguous original descriptions, especially the use of an unreliable diagnostic for petiole texture, *D. asperum* had been confused with *D. polyphyllum* for centuries (Zhu & Grayum, 1995). The names have been applied indiscriminately and have been used in different senses by different authors (Schott, 1858b; Engler, 1878, 1911; Jonker-Verhoef & Jonker, 1953). Specimens of the same taxon have been identified with either name in herbaria throughout the world. Through lectotypification and neotypification, Zhu and Grayum (1995) elaborated the concept of these two species. *Dracontium asperum* has spathe margins broadly overlapping and seed with a strongly interrupted dorsal ridge, while *D. polyphyllum* has spathe margins rarely overlapping and seed with a continuous dorsal ridge.

In 1865, Schott described the genus *Chersydrium* Schott on a single species, *C. jararaca* Schott, citing *D. asperum* as a synonym (Schott, 1865: 73). In the protologue, Schott noted that petiole armament is a variable character in *Dracontium*, but failed to provide any diagnostic for his new *Chersydrium*. Because *D. asperum* was cited as a synonym, according to the *Code* (Greuter et al., 2000, Art. 52.1) *Chersydrium jararaca* is superfluous, illegitimate, and to be rejected. Berthold Seemann (1869) described a new genus, *Godwinia* Seem., from Nicaragua with a single species, *G. gigas*, in honor of George Godwin. Masters (1873) later published a drawing of an inflorescence of *G.*

gigas and suggested the species would be more properly placed in the genus *Dracontium*, but he did not make the transfer. Engler (1877) agreed, and two years later (1879) established the combination *D. gigas* (Seem.) Engl., which synonymized *Godwinia*. An epitype, an interpretative type when all original material is demonstrably ambiguous (Greuter et al., 2000, Art. 9.7), represented the first taxonomic application of the concept in seed plants and was designated for the species by Zhu (1994a).

In his first classification of the family Araceae, Engler (1877) introduced his subfamily concepts with all presently recognized *Dracontium* species in subfamily Lasioideae, which is defined by assimilated leaves that persist for only one vegetative season. *Dracontium* remains a member of subfamily Lasioideae, although the modern classifications of the Araceae differ radically above the tribal level (Grayum, 1990; Bogner & Nicolson, 1991; Mayo et al., 1997; Keating, 2004). Following Engler (1877, 1920), *Dracontium* has been treated in the tribe Lasieae when tribes are recognized in the subfamily Lasioideae (Hay, 1992).

In his infrageneric classification, Engler (1889) recognized three sections: *Dracontium* sect. *Eudracontium*, including *D. polyphyllum* and *D. asperum*, characterized by a very short peduncle 5–18 cm long above ground and a relatively small spathe (6)10–20 cm long; *Dracontium* sect. *Godwinia*, with the single species *D. gigas*, with its long peduncle to 30–120 cm long and a relatively large spathe to 58–78 cm long; and *Dracontium* sect. *Echidnium*, presumably with a unilocular ovary, which was proven to be erroneous (Zhu, 1996).

Demonstrating his extraordinary knowledge of the Araceae, Engler (1905) described *D. longipes* and *D. pittieri* from Brazil and Costa Rica, respectively. In 1911, he published the only extant revision of the genus synonymizing *Ophione* and reinstating *Echidnium*. Twelve names in three genera were recognized: *Crytosperma spruceanum* (= *D. spruceanum*); *Dracontium asperum*, *D. carderi*, *D. costaricense*, *D. longipes*, *D. polyphyllum*, *D. purdieanum*, and *D. trianae* in section *Eudracontium*; *D. gigas* and *D. pittieri* in section *Godwinia*; and *Echidnium dubium* and *E. regelianum*. Ten of these species remain recognized in *Dracontium*.

Since Engler's landmark work in 1911, eight more names under *Dracontium* have been published. *Dracontium ulei* K. Krause was described from Acre, Brazil (Krause, 1914). *Dracontium soconuscum* Matuda was described from southern Mexico (Matuda, 1949). *Dracontium dressleri* Croat was described from Panama and was named in honor of Robert Dressler (Croat, 1975). *Dracontium margaretae* Bogner was described from Mato Grosso, Brazil, and was named in honor of Margarete Emmerich (Bogner, 1981). Three species were described by Bunting in 1986 and 1988, *D. aricuaisanum* G. Bunting, *D. changuango* G. Bunting, and *D. lineare* G. Bunting. Finally, *D. croatii* G. Zhu was described from the Andes in honor of Thomas Croat (Zhu, 1995).

Herein, 10 additional species are described: *Dracontium amazonense*, *D. angustispathum*, *D. asperispathum*, *D. bogneri*, *D. grandispathum*, *D. grayumianum*, *D. guianense*, *D. peruvianum*, *D. plowmanii*, and *D. prancei*.

Morphology and Anatomy

Tubers, Tubercles, and Roots

Tubers (Fig. 1). The size, weight, and morphology of tubers vary from one season to the next. Starch accumulates in the tuber to its maximum prior to inflorescence development, and is for the most part utilized during production of the inflorescence and new leaf. Diminution of the tuber is often associated with a change in its vertical depth rather than the horizonal diameter of the tuber. Since the tuber dimensions vary seasonally, hollow spaces in the soil are often seen both above (1–3 cm) and below (3–8 cm) the tuber. This upper space accommodates the growth of tubercles and contractile roots, while the lower hollow allows the tuber to settle deeper into the soil as the contractile roots dry out during dormancy. This settling may gain protection from corm-eating herbivores such as agoutis and peccaries. However, disturbances from these same animals are responsible for distributing the tubercles.

Tubercles (Fig. 1). Tubercles are borne on top of tubers, rarely on the side of irregularly shaped tubers in *D. margaretae*, and often mixed with roots. Tubercles allow *Dracontium* to reproduce vegetatively. They are usually dormant, activated only after disturbance. When a tuber is disturbed or broken off, tubercles start to change in shape, somewhat irregularly shortening, and produce their own shoot and roots.

Roots (Fig. 1). Primary roots of *Dracontium* emanate from the flattened apex of the tuber and grow downward in all directions, completely surrounding the tuber (Fig. 1B). Secondary roots start below the tuber apex and are subdivided into many smaller roots. The strong and often contractile root system functions not only in water and nutrient absorption, but also serves to support the plant. The roots hold the tuber in a position that facilitates the formation of the hollow spaces above and below the tuber.

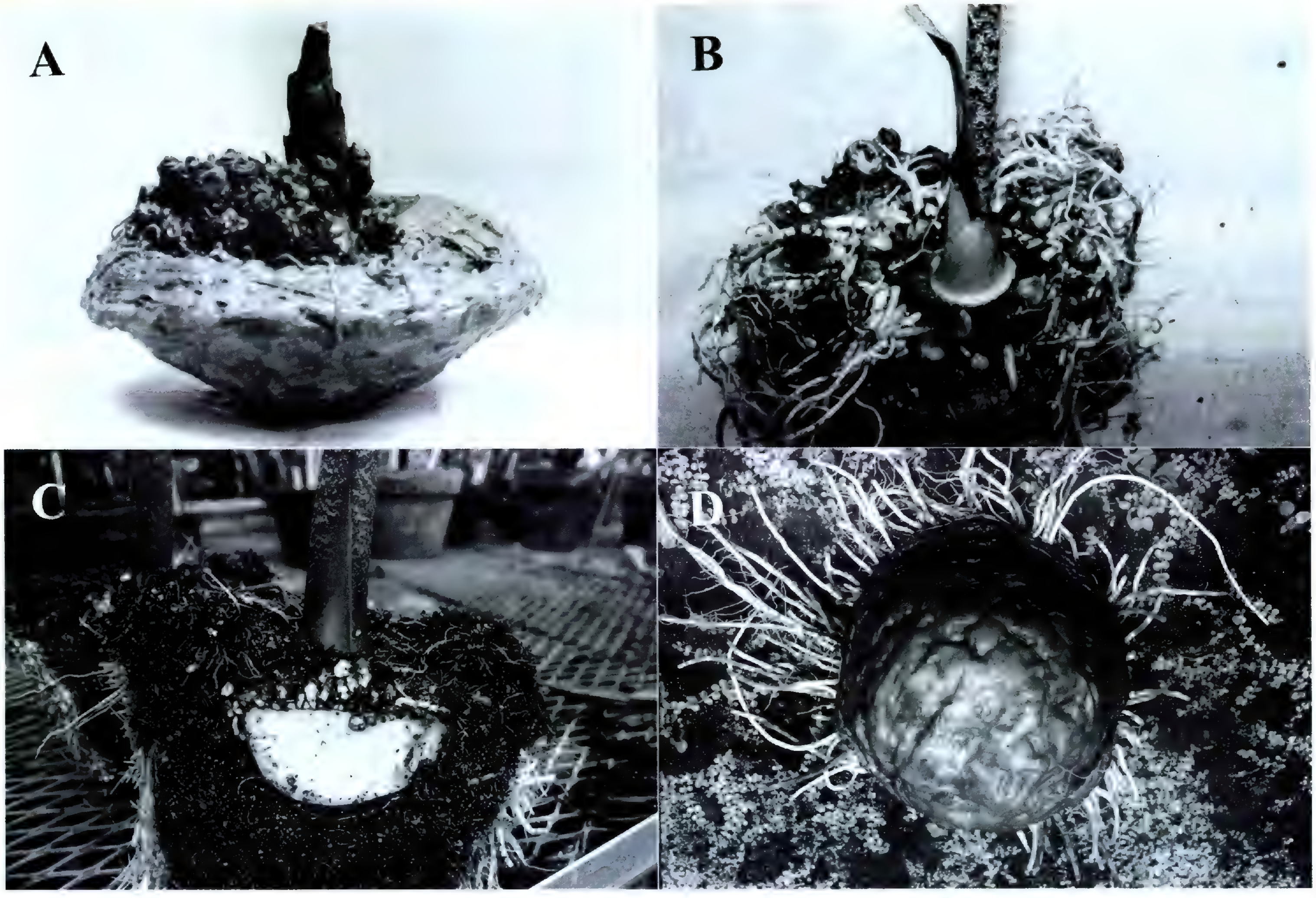

Figure 1. A–D, *Dracontium* tubers. —A. *D. plowmanii*. Tuber showing more or less flattened top with tubercules and rounded bottom. Photo by G. Zhu. —B. *D. polyphyllum* (*Croat 73867*). Tuber showing roots emerging from the apex of the tuber and clusters of tubercles. —C. *D. polyphyllum* (*Croat 56898*). Cross section of tuber showing typical shape with more or less flattened top and rounded bottom. —D. *D. grayumianum* (*G. Zhu & Croat 1506*). Lower surface of tuber showing rounded, smooth surface with the roots arising from the apical portion.

The tuber naturally assumes a deeper position when the roots dry out after each growing season.

LEAVES

Cataphylls. Cataphylls are the bract-like structures subtending the petiole, and usually completely embracing new growth from tubers after dormancy, often drying long before the leaf blade fully expands, and usually rotting away, becoming barely visible after the leaf blade has fully expanded.

Petioles (Fig. 2). The petioles of *Dracontium* are thick and aerenchymatous (Fig. 2A), frequently more than 2 m long. The exterior surface is often highly variegated (Fig. 2A, B), dark or purplish green, sometimes brown tinged, mottled with pale green or creamy areas suggesting a reptilian pattern (Fig. 2A, B). The mottled areas often appear as upward brush strokes, which originate from protuberances. Petiole surface texture is variable among species, from smooth textures to heavily beset with protuberances (Fig. 2B). The latter are often accompanied by horizontally elongate, irregular projections bordering two differently colored areas and sometimes also by spiny projections to 2 mm long. The proximal half of the petiole tends to have more protuberances or projections, while the distal half is much smoother. The aerenchyma cells of the petiole are cylindrical, hollow, to 6 cm long and 0.5 cm wide (Fig. 2C). The sheathing of the petiole is convolute, forming a closed space in the center through which the inflorescence or leaf initiates.

Blades (Fig. 2D). The tripartite leaf blade is held horizontally or ascending up to 45° from the petiole apex. Blade rachises may be mottled similar to the petioles but in much paler shades or may be concolored (Fig. 2D). They are usually smooth but may be armed with spiny projections, also similar to those of the petiole. The basal rachis of the middle blade division may be as long as the lateral divisions (*D. spruceanum*) or twice or more as long as these (*D. angustispathum* and *D. grayumianum*). Segments of *Dracontium* leaf blades can be entire or lobed, and can be distinguished on the basis of their position. Sometimes, there are rounded, triangular, or oblanceolate contrastingly small segments among the basal and medial segments. These small segments may be absent (*D. spruceanum*) or alternate with the larger segments (*D. soconuscum*), or more often found near the base of each leaf division (*D. polyphyllum*). They may be confluent with larger segments (*D. gigas*) or free (*D. spruceanum*). Likewise, medial and basal segments may be confluent or free from one another. The basal subdivisions of *Dracontium* consist of many smaller segments (*D. gigas* and *D. grayumianum*) or sometimes a single segment (*D. angustispathum*). The terminal subdivisions always consist of at least two segments in the lateral division and at least three segments in the middle division.

In the early development of a *Dracontium* leaf blade, all leaf divisions may point upward (*D. gigas*, Fig. 11A; *D. margaretae*, Fig. 16B), or the middle divisions may point upward while the lateral divisions point downward (*D. asperum*; *D. spruceanum*, Fig. 25A). Juvenile leaves of *Dracontium* are usually sagittate or sagittately lobed, rarely linear or trifid (*D. margaretae*).

INFLORESCENCES

Bracteoles (Figs. 4A, 4B, 8A, 16C, 17B, 24B). Bracteoles are the bract-like structure subtending the peduncle of each *Dracontium* inflorescence. The relative length of the innermost (also the longest) bracteole to the peduncle is an important character distinguishing species in *Dracontium*. It ranges from being much shorter than the peduncle (*D. plowmanii*) to longer than the peduncle (*D. prancei*). The bracteoles usually rot away soon after anthesis.

Peduncles (Figs. 7A, 8A, 11B, 13A). *Dracontium* inflorescences are produced before, or sometimes after, new leaf development. When inflorescences are produced right after a new leaf, they often appear as having developed simultaneously with the leaf, as sometimes in *D. croatii*, *D. pittieri*, and *D. spruceanum* (Fig. 25A). The fertile peduncles of *Dracontium* are usually shorter and thinner than the associated petiole and may be completely underground (*D. dubium*) or nearly as long as the petiole, rarely exceeding the petiole (as sometimes in *D. spruceanum*). Peduncles are much like the petioles in terms of coloration and armament.

Spathe (Figs. 4A, 4B, 7A, 9A, 9B). The shape and size of the spathe distinguish species of *Dracontium*, perhaps more so than any other character. The spathe is marcescent and often disintegrates on a developed infructescence. At anthesis, the length of the spathe in the genus may range from a few cm long and 1 cm wide as in *D. bogneri* to as much as 85 cm long and 20 cm wide as in *D. gigas*. Spathes may be more or less hooded and boat-shaped (*D. asperum*, *D. gigas*, and *D. pittieri*) or suddenly contracted at a certain point and gradually acuminate distally (*D. angustispathum*, *D. dubium*, *D. purdieanum*, and *D. spruceanum*). The spathe margins may be broadly overlapping near the base forming a bell-shaped tube and broadly

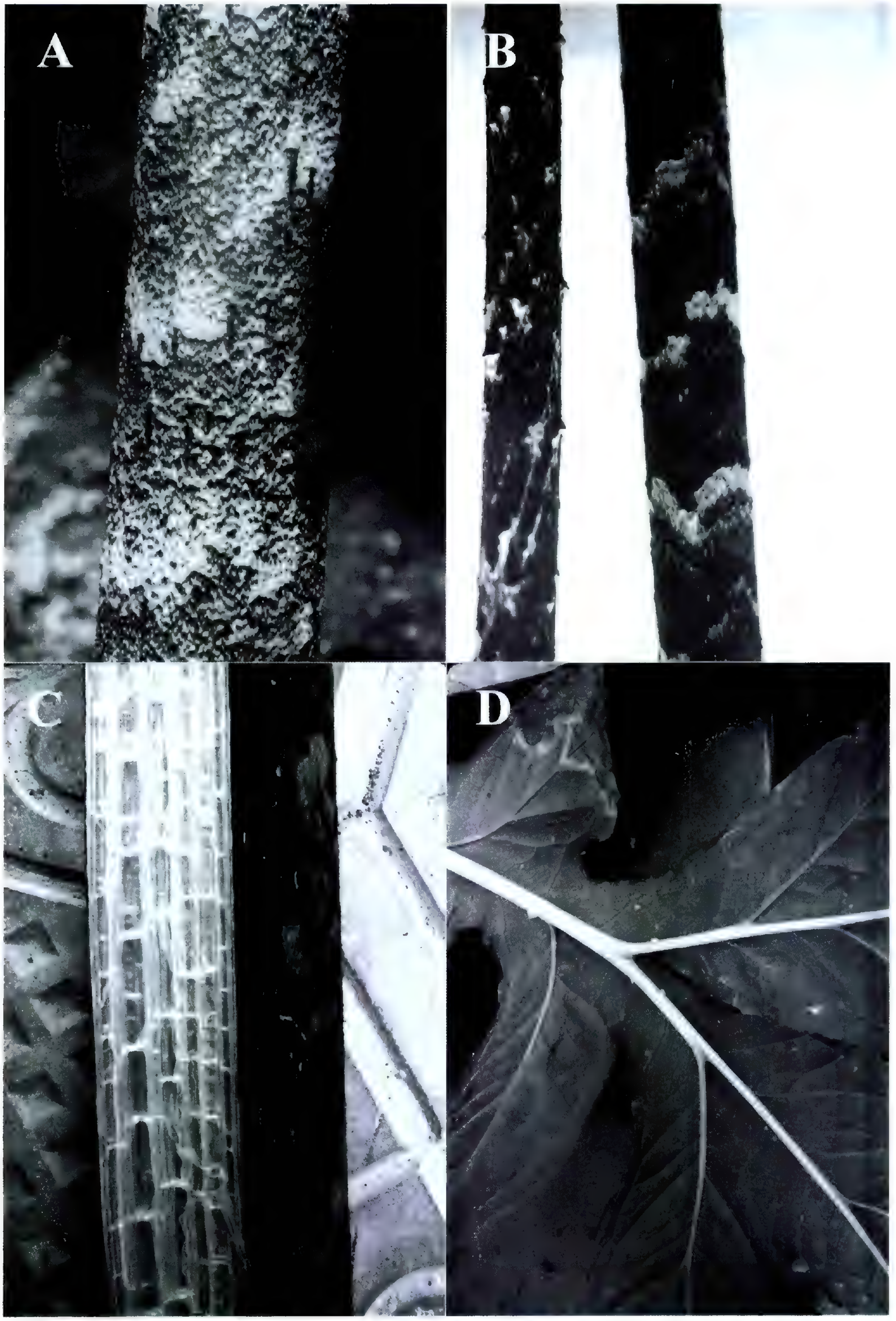

Figure 2. A–D, Petioles and blade. —A. *Dracontium grayumianum* (*G. Zhu & Croat 1506*). Close-up of petiole showing variegation. —B. *D. croatii* (*Croat 72368*). Petioles showing variegation and short spines. —C. *D. gigas* (*G. Zhu 1156*). Petioles showing exterior surface and inner surface with aerenchymatous cells. —D. *D. croatii* (*Croat 72368*). Lower surface of leaf blade showing the prominently round-raised medial ribs and pinnately lobed lateral veins.

open above as in *D. grayumianum*, *D. purdieanum*, and *D. soconuscum*. They broadly overlap at the lower ⅓ to ⅔ with only a narrow opening above (*D. gigas* and *D. prancei*), or barely overlap (*D. pittieri* and *D. polyphyllum*). The apex of the spathe is variably acuminate and ranges from erect or slightly arching as seen in *D. angustispathum*, *D. polyphyllum*, and *D. spruceanum* to strongly arching to perpendicular in *D. amazonense* and *D. asperum*.

The outer surface of the spathe is often matte, with many elongate clumping projections. The spathe may be maroon, tinged green (*D. spruceanum*), purplish red or olive-brown (*D. polyphyllum*), green (*D. croatii* and sometimes *D. spruceanum*), or sometimes with a basal paler area on the abaxial side (*D. asperum*). The inner surface may be glossy (*D. angustispathum* and *D. plowmanii*) or semiglossy (*D. gigas* and *D. pittier*) or covered with densely overlapping translucent scales (*D. dubium* and *D. purdieanum*). Spathe inner surface is maroon (*D. polyphyllum*), maroon tinged reddish (*D. asperum* and *D. soconuscum*), or reddish brown to olive-brown (*D. spruceanum*). There is usually a creamy white translucent area at the spathe base that may be obscure (*D. asperum*, *D. polyphyllum*, and *D. ulei*) or to 1 to 3 times as long as the spadix in height (*D. asperispathum*, *D. grandispathum*, *D. pittieri*, and *D. spruceanum*). The inner surfaces of the spathe are often covered with whitish or brownish spotted gland-like structures associated with the stomata. These structures appear to control the emission of scent (see section on Phenology and Pollination).

Spadix (Figs. 3D, 4C, 7B, 11C). The spadix of *Dracontium* is sessile, or stipitate to 0.5–2.5 cm long. It ranges from 1 to 9 cm long and 0.5 to 2 cm diam. at anthesis, and from 4 to 25 cm long and 4 to 10 cm diam. when fruiting. The color of the spadix corresponds to the color of the tepal apices and styles, which may be dark purple, green, light brown, or rarely gray. The spadix may be hidden at anthesis (*D. croatii*, Fig. 9A, *D. gigas*, *D. spruceanum*, and *D. asperum*) or exposed naturally (*D. polyphyllum*, Fig. 21A, *D. pittieri*, *D. soconuscum*, Fig. 24A, *D. purdieanum*, Fig. 23A, and *D. dubium*). A spadix may be typically cylindric (Fig. 11C), rarely globose, or sometimes cylindroid-tapered (Fig. 22B). Sometimes 1 to 5 tepals at the apex of the spadix are elongated into 0.5–1 cm appendages (*D. dubium*, *D. grayumianum*, *D. purdieanum*, and *D. soconuscum*, Fig. 3D). The function of these appendages is unknown. The central axis of the spadix consists of aerenchyma, similar to those seen in the petioles and peduncles.

FLOWERS

The flowers of *Dracontium* are arranged spirally on the spadix. Each consists of a perianth, a single pistil, and 4 to 19 stamens (Fig. 3B, C). The perianth consists of 4 to 8 fornicate tepals that envelope the pistil and stamens at anthesis. The apices of the tepals are green to purple and covered with yellow-tinged raphide cells. The lower portion of each tepal is often transluscent, white to light brown, sometimes with red or red-purple dots.

Stamens (Fig. 3C). The filaments are elongate, often slightly dilated, subcompressed, and abruptly contracted at the apex into the connective. The anthers exceed the connective and are linear-elliptic in shape. They are often yellow, turning reddish brown, sometimes with dark purple, especially near the aperture, after anthesis. The anthers are usually hidden before anthesis and dehisce apically by a vertical slit with a more or less rounded aperture at anthesis (Fig. 26B). Pollen emerges from these apertures in a strand that reaches the stigma, and is as long as or longer than the style. The function of these pollen strands is discussed in the section on reproductive biology.

Pistils (Fig. 26A). The ovaries in *Dracontium* are narrowly ovoid, pale green, and incompletely 2- to 5-loculed, with axile or basal placentation. The ovules are solitary in the locules and amphitropous or campylotropous. The style is 0.5–5 mm long above the tepals at anthesis. It is dark purple to pale green, and persistent or caducous. The stigmas (Fig. 26A) are unlobed or variably up to 4-lobed, usually covered with a translucent sticky liquid at anthesis but drying out afterward. Ovaries are ovoid, pale green, incompletely 2- to 5(7)-loculed with axile or basal placentation. Ovules are one per locule, amphitropous or campylotropous.

FRUITS AND SEEDS

Fruits. The berries of *Dracontium* may be globose (*D. croatii*, Fig. 9C; *D. spruceanum*), angularly subglobose with three to six angles (*D. grayumianum*, Fig. 13C; *D. longipes*, Fig. 15B); or elongate with a projection (*D. angustispathum*). They range from having one seed (*D. angustispathum*) to as many as seven seeds (*D. polyphyllum*). The young berries are usually green, while the mature berries may be orange (*D. angustispathum*, *D. dubium*, *D. croatii*, *D. gigas*, *D. grayumianum*, *D. peruvianum*, *D. pittieri*, and *D. spruceanum*), purple tinged (*D. asperum*), green tinged purple (*D. bogneri*, *D. polyphyllum*), red or purple-red (*D. margaretae* and *D. purdieanum*), or purple-brown (*D. soconuscum* and sometimes *D. gigas*). The berries are usually

darker apically and may be depressed around the persistent style (*D. bogneri*, *D. dubium*, and *D. soconuscum*) or rounded (*D. angustispathum* and *D. spruceanum*). The berries are often covered with small whitish raphide cells and sometimes, red dots.

Seeds. *Dracontium* shows great diversity in seed morphology, and this is of great value for species distinction in the genus. Seed size ranges from 3 mm wide (*D. bogneri*) to more than 11 mm wide (*D. croatii* and *D. peruvianum*) with only a trace of endosperm present. The seeds may be rounded (*D. croatii*, *D. gigas*, and *D. pittieri*), elongate (*D. spruceanum* and *D. grayumianum*), reniform (*D. polyphyllum* and *D. plowmanii*), or more or less triangular (*D. asperum*). They are more or less laterally compressed, with the sides either convex (*D. polyphyllum*) or depressed (*D. asperum*). The sides of the seeds may be smooth (*D. polyphyllum*, *D. asperum*, and *D. bogneri*) or decorated with small wart-like projections (*D. spruceanum*). The seeds typically have three dorsal ridges (*D. gigas*, *D. pittieri*, *D. peruvianum*, and *D. spruceanum*), but sometimes have only one (*D. polyphyllum*, *D. asperum*, and *D. plowmanii*) or none (*D. bogneri*). The dorsal ridges may be continuous (*D. polyphyllum* and *D. plowmanii*) or strongly interrupted (*D. dubium*, *D. croatii*, and *D. grayumianum*), and either thin (*D. grayumianum*) or thick (*D. croatii*, *D. gigas*, and *D. peruvianum*).

Chromosome Numbers

All species of *Dracontium* that were examined are diploids with $2n = 26$, the only number known in the tribe Lasieae (Petersen, 1989). These counts of $2n = 26$ were confirmed by the first author in *D. amazonense* (*G. Zhu 1454*), *D. gigas* (*Bogner 1267*), *D. polyphyllum* (*Croat 74210*), and *D. prancei* (*Croat 73867*), using the method mentioned in Petersen (1989). Counts were made from root tips in all cases. *Dracontium* has comparatively small chromosomes, similar to those of other members of the same tribe. Petersen (1989) showed that chromosome size and number are highly variable in the Araceae and of great importance for their taxonomy and evolution at the generic level. However, based on the *Dracontium* chromosomes seen thus far, they appear to be of little taxonomic value at the specific level owing to their similarity in number, size, and shape.

Distribution and Habitats

Distribution. Species of *Dracontium* occur from 15°22′N latitude in the Mexican district of Soconusco in Chiapas State (*D. soconuscum*), south through Nicaragua, Costa Rica, Panama, the Dominican Republic and Puerto Rico, Colombia, Venezuela, Trinidad, West Indies, the Guianas, Ecuador, Peru, Bolivia, and Brazil to the Tropic of Capricorn in Paraguay. In South America, the eastern limit of the collections is 44°28′W longitude in Maranhão, Brazil; *Dracontium* extends west along the Pacific coast of Colombia, Ecuador, and Peru. No collections of *Dracontium* are known from Cuba, Chile, Argentina, or Uruguay.

Five species occur in Mesoamerica: *Dracontium gigas*, *D. grayumianum*, *D. pittieri*, *D. soconuscum*, and *D. spruceanum*. *Dracontium soconuscum* is the only species known from Mexico and the northernmost species of the genus. This species also occurs in Costa Rica and Panama, and is very likely to occur also in Guatemala, El Salvador, and Nicaragua. *Dracontium gigas* is the only species known from Nicaragua; it is also known from the Atlantic slope of Costa Rica in the provinces of Alajuela, Heredia, and San José. All Mesoamerican species besides *D. grayumianum* occur in Costa Rica, including *D. pittieri*, endemic to the Pacific slope in the province of Puntarenas. It has not been collected in adjacent Panama, where three other species occur, *D. soconuscum*, *D. spruceanum*, and *D. grayumianum*. *Dracontium soconuscum* has its southern geographic limit in the Panama Canal area; to the south it is replaced by *D. grayumianum*, which has a typical Caribbean/Chocó distribution pattern as encountered in *Philodendron* species (Grayum, 1996).

Dracontium spruceanum is the most widespread species of the genus, ranging from Costa Rica, through Panama, Colombia, into northwestern Ecuador and along the eastern slope of the Andes through Amazonian Ecuador, Peru, and northwestern Amazonian Brazil. It is the only species of *Dracontium* that occurs on both slopes of the Andes, having been collected on the western slope of the Andes in Chocó Department, Colombia, and western Ecuador. Species diversity of *Dracontium* is highest in the Guianas (including the adjacent Venezuelan and Brazilian Amazonian regions), which have seven species (*D. amazonense*, *D. asperum*, *D. dubium*, *D. guianense*, *D. nivosum*, *D. prancei*, and *D. polyphyllum*). A secondary center of diversity of *Dracontium* is in Amazonian Peru (Loreto), where five species (*D. amazonense*, *D. angustispathum*, *D. asperispathum*, *D. peruvianum*, and *D. spruceanum*) coexist.

Eight of the 23 South American species herein of *Dracontium* appear as narrow endemics, often known only from a few localities (*D. bogneri*, *D.*

dubium, *D. guianense*, *D. longipes*, *D. nivosum*, *D. polyphyllum*, *D. prancei*, and *D. ulei*). Some of these relatively narrowly ranging species are slightly more widespread, such as *D. amazonense*, which ranges from Amazonian Peru to Amazonian Brazil. Only one species, *D. asperum*, occurs in the Dominican Republic and Puerto Rico; it is also found in the Guianas and the islands of Trinidad and Tobago. In South America, Brazil has the largest contingent of *Dracontium* species, with 11 plus 2 additional species likely to occur there (*D. guianense* and *D. plowmanii*).

Species of *Dracontium* typically occur from near sea level to about 500 m. West Andean *D. croatii* is an Ecuadorian endemic species and is known only from higher elevations, from 800 to 1200 m. A few species may range from quite low elevations to high elevations. These include *D. pittieri* (30–1000 m), *D. grandispathum* (250–1200 m), and *D. spruceanum* (25–1215 m).

Habitats. Species of *Dracontium* occur in habitats from *Premontane moist forest* (P-mf), *Tropical moist forest* (T-mf), *Premontane wet forest* (P-wf), and *Tropical wet forest* (T-wf). Most of the species occur only in one life zone: *D. amazonense*, *D. dubium*, *D. guianense*, *D. margaretae*, *D. prancei*, and *D. ulei* in *Tropical moist forest* (T-mf); *D. gigas* and *D. grayumianum* in *Tropical wet forest* (T-wf). Some species occur in two life zones (*D. angustispathum*, *D. asperispathum*, *D. bogneri*, *D. croatii*, *D. gigas*, *D. grandispathum*, *D. longipes*, *D. nivosum*, *D. pittieri*, *D. plowmanii*, *D. polyphyllum*, and *D. purdieanum*). *Dracontium asperum*, *D. peruvianum*, *D. soconuscum*, and *D. spruceanum* are the only ecologically widespread species, all having been collected in three different life zones.

Dracontium plants tend to occur along forest margins and in somewhat disturbed or wasted areas that are usually seasonally wet. Only one species, *D. margaretae*, is found growing in seasonal swamps.

Reproductive Biology

Phenology and Pollination

Inflorescences in *Dracontium* are often produced before new leaf production (*D. soconuscum*). They may sometimes appear simultaneously with new leaf production as in *D. croatii*, *D. pittieri*, and *D. spruceanum*. Some species produce inflorescences throughout the year (*D. spruceanum*), while others bloom in the wet season (*D. grayumianum* and *D. pittieri*) or in the dry season (*D. gigas*). These inflorescences usually last four to six weeks, then the spadix elongates into an infructescence if pollinated. The berries usually mature in a few to several months, with 9 to 11 months noted in *D. asperum* (J. Boos, pers. comm.).

The flowers of *Dracontium* are protogynous and mature basipetally (Poisson & Barabé, 1998). For a single flower, the ovary is anthesal usually one to two weeks prior to anther dehiscence. It often takes two to four weeks for all the flowers on a single spadix to reach anthesis. The appearance of the stigmatic fluid signals the receptive maturity of the ovary, often before the anthers of the same flower have dehisced. The disappearance of the stigmatic fluid signals that the stigma is no longer receptive. The anthers of mature stamens dehisce along an apical slit to form more or less rounded apertures. The pollen exits in cohesive strands that contract the stigma and its associated style (Fig. 26). The pollen may be carried away by pollinators or may fall naturally when dry onto a receptive stigma at a lower position on the same spadix. Flowers at the apex of the spadix must have pollen from other plants in order to be pollinated.

This protogyny in *Dracontium* (common throughout the family) serves to insure cross pollination. Hand pollination for *D. asperum* was reported in cultivation by Hans Boos in Trinidad, West Indies. In this case the inflorescence produced berries when cross pollinated and withered when there was no pollen from another inflorescence available (J. Boos, pers. comm.). When cultivated in the Missouri Botanical Garden greenhouse, *D. polyphyllum* developed young berries with only one inflorescence blooming. However, no berries ripened before the infructescence rotted away. Two other species, *D. amazoense* and *D. prancei*, have been hand pollinated by the senior author in the Missouri Botanical Garden research greenhouse; both plants failed to form berries. Another attempt at hand pollination between these two species also failed. Future reproductive studies are certainly needed in the genus.

At anthesis, the spathe of *Dracontium* emits a foul odor reminiscent of rotting meat, dead fish, or decomposed vegetables. The timing and duration of scent emission differ among species. Some species release their scent from early in the morning until late in the afternoon (*D. gigas* and *D. polyphyllum*), others from late in the morning until early in the afternoon (*D. soconuscum*), while others emit scent from afternoon to late evening (*D. croatii*) for approximately a six-hour period (Guanghua Zhu, pers. obs.). When the spathe is removed from the inflorescence, the scent vanishes, indicating that the scent is produced by the spathe instead of the spadix, as is commonly believed. Under SEM, there

are many structures associated with stomata on the inner spathe surface, sometimes also on its outer surface. These structures may be osmophores responsible for the emission of scent. The stomata may be found opened or closed.

The pollinators of *Dracontium* remain unknown. Croat (1975) suggested that *Dracontium* has a typical fly-pollination syndrome because of the trap-like nature of the spathe of some species and the foul scent the plants emit during anthesis, which is typical of other fly-pollinated species in the Araceae. Houseflies and some fruit flies were observed to visit the flowers in the greenhouse; however, these were also the only insects present in the greenhouse. Flies and beetles were reported as visitors of *D. gigas* when it was blooming at La Selva, Costa Rica (M. Grayum, pers comm.). Large metallic blowflies are reported to have visited *D. asperum* in Trinidad as well as in Florida (J. Boos, pers. comm.).

Reproduction and Dispersal

Vegetative reproduction is by tubercles produced at the apex of the tuber or via the production of a tumor-like structure, which is part of the tuber body. Tubercles are the most important means of vegetative reproduction in *Dracontium*; they typically remain dormant for several years. Tests conducted in North Carolina have shown that they may remain dormant for two years despite different treatments, including wounding, treatment with growth hormones, use of different soils and different temperatures (P. Schmidt, pers. comm.). However, disturbed tubercles may sometimes enlarge and produce a leaf. Concomitantly, the principal tuber usually rots away and is replaced by several smaller plants originating from these tubercles. Sometimes the smaller plants from tubercles may grow simultaneously while still attached to the parent for several seasons before detaching from the principal tuber.

All species of *Dracontium* are known to produce berries and seeds in the wild. However, there is a tradeoff between vegetative and sexual reproduction. When a plant regularly produces inflorescences and leaves (often alternately), its tubercles generally remain dormant. A disturbance to the principal tuber often causes its tubercles to enlarge and to produce a plantlet; the principal tuber ceases inflorescence production and instead produces only leaves.

Populations show high sociability with remarkable densities exhibited by *D. gigas* and *D. grayumianum*. Individual clusters with many small plantlets can be found within a few meters from the parent plant. This suggests that short-distance dispersal via tubercules occurs in these species. Croat (pers. comm.) suggested that *Dracontium* tubers may be harvested by wild pigs because of their starch content. At La Selva, a clump of *D. gigas* was found near an agouti nest. The agouti's digging may have been responsible for the short-distance dispersal of this species. However, there was no evidence that this animal was eating the tuber. The tubercles of *Dracontium* easily detach from the parent tuber when it is harvested or disturbed. Due to their small size, the tubercles can be transported easily in dirt when dug up. This theory is not in conflict with the fact that many plants of *Dracontium* are found as single individuals before reaching the stage of sexual reproduction. As stated earlier, tubercles remain dormant if the plant is not disturbed, and the long-distance dispersal of seeds by birds and mammals may result in an individual plant growing in a new location away from the mother plant. Long-distance dispersal of *Dracontium* seeds is still unstudied, but the genus has a typical bird-dispersal syndrome with colorful but non-aromatic fruits and seed, which can be individually pecked out of an infructescence. However, some *Dracontium* berries, e.g., those of *D. grayumianum*, have a pleasant fruity scent and sweet taste, which is typical of a mammal-dispersed seed syndrome.

Uses

The ethnobotanical uses of *Dracontium* were summarized by Plowman (1969) and later by Croat (1994). Many *Dracontium* species are utilized by indigenous people, including those of Hispanic culture, as having edible parts and possessing medicinal uses. One of the most common medicinal uses of these plants is in the treatment of snakebite, documented for *D. asperum*, *D. grayumianum*, *D. pittieri*, *D. polyphyllum*, and *D. spruceanum*. The method of aroid medicinal usage varies in different areas. Roots and petioles of *D. asperum* are crushed with sugar and alcohol yielding a tincture, which is consumed at regular intervals for snakebite in Brazil (Plowman, 1969). The remaining pulp is applied to the area of snakebite by the same people (Croat, 1994). Leaf infusions of *D. pittieri* were ingested and applied externally as a remedy for the poisonous bite of the bocaraca snake (*Bothreichis schlegelii* Berthold) by indigenous peoples of Puntarenas, Costa Rica (Pittier, 1957). The Bribri Indians of Costa Rica first boil an infusion of *D. pittieri* or

D. soconuscum leaves, then apply this to snakebite wounds after cooling (Ginzbarg, 1977).

Dracontium spruceanum has been used extensively by indigenous peoples. Pulp from scraped tubers or split petioles of this plant is used by the Mayna Indians of Peru and applied directly to wounds (Croat, 1994). The scraped tuber and unheated inflorescences (or infructescence) are used by the Achuar Indians of Peru to massage snakebite, while the pulp of the scraped tuber is also applied to boils (Croat, 1994). The Achuar also use the crushed tuber of this plant mixed with equal parts of two *Solanum* (Solanaceae) species ("untukar" and "syukahuito") to alleviate boils and to make tumors recede (Croat, 1994). Tubers of *D. spruceanum* are also cooked and eaten to relieve chest pain in Peru (Croat, 1994). Steward and Metraux (1948) reported that leaves of *D. spruceanum* (as *D. longipes* Engl.) were rubbed on snakebite wounds by the Amahuaca Indians of Ecuador. Schultes and Raffauf (1990) reported that plants of *D. longipes* Engl. were cultivated by the Kofán Indians of Colombia and Ecuador and used in a decoction for treating diarrhea. They further reported that in Peru, tubers of these plants are ground into a paste, wrapped in *Calathea* (Marantaceae) leaves, warmed in a fire, and applied to snakebite.

Other medicinal uses have been reported for *Dracontium*. The powdered tuber of *D. asperum* has been used to treat the effects of asthma, anemia, amenorrhea, and whooping cough (Peckolt, 1892; Le Cointe, 1934). Juice from the tubers of this species is used to kill maggots in animals (Plowman, 1969). In Trinidad, *D. asperum* tubers have been harvested as a substitute for potatoes after a period of drying in storage (Boos & Boos, 1993). Tubers of *D. grayumianum* are ground with water and used by Chocó Indians in Panama for treating hemorrhaging during childbirth (Croat, 1994). An infusion of the leaves of *D. pittieri* is used to kill maggots on wounds (Pittier, 1957). In addition to being used as a snakebite remedy (Plowman, 1969), *D. polyphyllum* is used as a remedy for hemorrhoids (Croat, 1994) and as an antidote for the venom of spiders and stingrays (Levi-Strauss, 1952). The tubers of *D. longipes* are ground and used as a paste applied to snakebites in Brazil (Plowman, 1969). Tubers of some species of *Dracontium*, such as *D. soconuscum* and *D. asperum*, are edible. They may be boiled and served like a potato or ground with water and consumed as a juice (Croat, 1994).

Some species of *Dracontium* have horticultural value and are favored by tropical gardeners and aroid nurseries because of the snakelike patterning of their petioles and the umbrella-like cut leaf blades. Most are easy to grow and can be vegetatively propagated by their tubercles. Several species were described from cultivated plants, including *D. polyphyllum*, *D. asperum*, *D. croatii*, and *D. gigas*. *Dracontium gigas* has been well known and commonly cultivated in European gardens since its discovery in Nicaragua in 1869. Since then, this species has been repeatedly described and illustrated in gardening publications and featured in plant exhibits (Seemann, 1869; Hooker, 1873; Masters, 1873; Watson, 1901; Macmillan, 1956). Other species, including *D. amazonense*, *D. prancei*, *D. soconuscum*, and *D. spruceanum*, are in cultivation in botanical gardens in Germany, the Netherlands, the United Kingdom, and the United States, as well as in private nurseries in Florida. The market for these plants is growing with increasing knowledge of the genus.

Relationships

Several general trends can be observed from our study of *Dracontium*, as well as from unpublished analysis of 58 different character states. Some species pairs share much in common. These include: (1) *Dracontium amazonense* and *D. prancei*; (2) *D. grayumianum* and *D. soconuscum*; (3) *D. dubium* and *D. purdieanum*; (4) *D. gigas* and *D. pittieri*; (5) *D. angustispathum* and *D. guianense*; and (6) *D. asperispathum* and *D. spruceanum*. In addition, *Dracontium margaretae* is clearly related to *D. amazonense* and to *D. prancei*. *Dracontium grandispathum* is most closely related to *D. asperispathum* and *D. spruceanum*. *Dracontium grayumianum* and *D. soconuscum* are often grouped together with *D. dubium* and *D. purdieanum*. Our studies indicate no infrageneric groups in the genus, but two major clades are suggested. Morphologically, these two clades can be distinguished by their peduncles. All species with subterranean peduncles or with peduncles only a few centimeters above ground level group in one clade (short-peduncle clade), while those with a peduncle more than 30 cm long above ground level, with only one exception, group in the other clade (long-peduncle clade). Our preliminary investigation also suggested an evolutionary trend from long peduncles to short (usually subterranean) peduncles within *Dracontium*. The most basal members of the genus are *D. angustispathum* and *D. guianense*, while the most advanced members are *D. amazonense* and *D. prancei*. The member with the most distinctive leaf blade of the genus, *D. margaretae*, is also among the advanced group.

Taxonomic Treatment

Dracontium L., Sp. Pl. 967, 1753. TYPE: *Dracontium polyphyllum* L. (lectotype, designated by Britton & Wilson (Scientific Survey of Puerto Rico and the Virgin Islands, 5(1): 7, 1923)).

Eutereia Raf., Fl. Tellur. 4: 12. 1836 [1838]. TYPE: *Eutereia nigricans* Raf.
Echidnium Schott, Oesterr. Bot. Wochenbl. 7: 62. 1857. TYPE: *Echidnium schomburgkii* Schott.
Ophione Schott, Oesterr. Bot. Wochenbl. 7: 101. 1857. TYPE: *Ophione purdieana* Schott.
Chersydrium Schott, Oesterr. Bot. Z. 15: 72. 1865. TYPE: *Chersydrium jararaca* Schott.
Godwinia Seem., J. Bot. 7: 314, t. 96, 97. 1869. TYPE: *Godwinia gigas* Seem.

Terrestrial, tuberous, perennial herbs, 1–5 m tall, with 1 leaf (rarely 2) and with 1 (or rarely 2) inflorescences, arising from an underground tuber buried 5–75 cm deep; *tuber* ± hemispheric, 2–20 cm diam., 2–10 cm thick; flat above, with a few to many tubercles among many roots; convex below, smooth or strongly wrinkled, without tubercles and roots; tubercles elongate, ovoid to ellipsoid or cylindrical and often laterally compressed, 0.5–3 × 0.5–1 cm, light brown; *cataphylls* 3 to 5, the innermost the longest, 2–20 cm long above ground, partially covering the petiole base, white-tinged pink or light brown (especially near the apex). *Leaves* solitary or sometimes more, arising terminally from tuber apical bud, tripartite; *petioles* 1–5 m long, 2–8 cm diam. at base, 1–3.5 cm diam. at apex, light to dark or brownish green, sometimes tinged brown near the base, mottled and streaked with whitish or pale green areas forming a reptilian pattern; armament varying from a smooth surface to having heavy protuberances, sometimes with horizontal elongate irregular projections bordering 2 differently colored areas, sometimes with spiny projections to 2 mm long; lower half of the petiole with more protuberances or projections, smoother above; *blades* with 3 major divisions, each 0.5–1.5 cm long, papyraceous to thinly coriaceous; upper surface green, glossy or less glossy, rarely matte; lower surface semiglossy or matte; sometimes with fenestrations along rachises or major veins; middle division sub-dichotomously divided into 3 sections; lateral divisions sub-dichotomously divided into 2 sections; each section may comprise a single leaf segment or be subdivided into 2 or 3 smaller subsections accordingly; *midrib* and major veins convex and light green on upper surface and conspicuously round-raised and paler on lower surface; secondary veins ± parallel and arching apically, forming 2 collecting veins along the margins, with the innermost the strongest; terminal segments 8–20 × 3–7 cm, lanceolate to irregular, free or confluent at base, often strongly decurrent downward along rachises, apically acuminate or caudate gradually into 1, 2, or rarely 3 apices; smaller leaflets oblanceolate or ± triangular, 1–15 × 1–6.5 cm, caudate, acute or rounded at apex, free at base, or decurrent downward partly covering the rachises, or confluent completely at base with rachises completely covered by leaf tissue; irregular or often pinnately arranged on the rachises; rachises mottled similar to petiole in a much paler shade or uniformly light green, sometimes tinged brown, smooth or armed as petiole; length from petiole apex to the first terminal subdivision of the middle division as long as or to twice as long as lateral divisions. *Inflorescence* solitary (rarely 2) arising from apex of tuber before or after leaf development; bracteoles 3 to 5, white-tinged pink to dark brown, acuminate contracting to an apiculate apex; the longest one (the innermost) completely covering the underground part and the base of the peduncle, sometimes longer than the peduncle and partly covering the spathe; *peduncle* reaching to slightly surmounting ground level, to 2.5 m long, often shorter than petiole, rarely exceeding petiole, 0.5–6 cm diam., much like the petiole in appearance when not covered by cataphylls, but tending to be smoother; coloration similar to that of petiole, sometimes more rose or brown; *spathe* marcescent, degrading on developed infructescence, narrowly ovate to naviculiform, convolute at base, open above, often hooded to broadly open; margins not overlapping or overlapping at the base and forming a tube, to broadly overlapping with only a small apical opening; ± acuminate at apex, erect to slightly arching (less than 45°) to strongly arching (45°–90°), externally violet-purple, often tinged green or greenish, with obvious raphide cells, often raised, sometimes with surface somewhat bullate, internally reddish purple to maroon, glossy to semiglossy, sometimes with thin dry scales, often with stomata surrounded by whitish or brownish spotted glands, often with a whitish translucent area 0.5–10 cm high around the base of the spadix, periodically emitting at anthesis a foul scent like decomposing vegetables or meat; *spadix* at anthesis greenish to purple, cylindric (sometimes thinner at apex), sessile or stipitate with a stipe 0.5–2.5 cm long; spadix of infructescence 4–25 × 4–10 cm, often 4 to 15 times longer and 4 to 8 times wider than at anthesis. Flowers perfect, perigoniate, and spirally arranged on spadix, opening basipetally; tepals 4 to 6(8), green to purple, completely covering anthers before anthesis. Stamens (4)5 to

17(19); anthers yellow, open apically, turning red-brown, sometimes with dark purple especially near the opening after anthesis; filaments often slightly dilated, subcompressed and abruptly contracted at the apex into the connective; anthers exceeding connective, linear-elliptic, yellow, turning reddish brown, sometimes with dark purple, especially near the aperture, after anthesis, dehiscing apically by a vertical slit with rounded aperture at anthesis; pollen emerging in strands; ovary of 2 to 5(7) locules each with 1 ovule; style 2–5 mm long above tepals at anthesis, pale green to dark purple, persistent in fruit or not; stigmas 2- or 3-, sometimes 4-lobed, covered with a clear sticky liquid at anthesis. *Berries* green when young, maturing to reddish, purplish, purplish red, purple-brown or orange, covered with small whitish raphide cells, sometimes with red dots (easily visible at 10×), darkened apically, somewhat depressed around style when persistent or rounded; *seeds* 1 to 7 per berry, variable in shape from round to reniform to triangular to elongate, 0.5–1.0 cm long, 0.4–1.2 cm wide, smooth or decorated dorsally with warty projections, usually with 1 to 3 dorsal ridges, these continuous or interrupted, thin or thick. Chromosome number: $2n = 26$ on all species counted to date.

Key to the Neotropical Species of *Dracontium*

1a. Blade segments linear, 1–1.5 cm wide, usually ascending at 45° angle from the petiole; growing in seasonal swamps; Venezuela (Apure and Guárico), Brazil (Mato Grosso do Sul), and Paraguay ..... 13. *D. margaretae* Bogner

1b. Blade segments not linear, 3–12 cm wide, spreading horizontally (or ascending at 45° angle from the petiole when young); growing in habitats other than seasonal swamps; southern Mexico to central Paraguay.

2a. Peduncle completely subterranean or not more than 10 cm above ground level; longest bracteole reaching to base of or covering to ½ of the spathe.

3a. Spathe cymbiform (boat-shaped), not at all constricted; spadix lacking appendages at apex.

4a. Spadix often concealed by spathe at anthesis; spathe margins broadly overlapping at the base for at least ½ of the spathe.

5a. Spathe 28–35 cm long, 6–10 cm wide at anthesis; endemic to Pará and Maranhão, Brazil ..... 14. *D. nivosum* (Lem.) G. Zhu

5b. Spathe to 20 cm long and 4.5 cm wide at anthesis; Brazil, Venezuela, and Peru.

6a. Inner surface of spathe semiglossy to velvety, never with translucent scales.

7a. Spathe usually less than 13 cm long, arching toward apex by 45° to 90°; lacking an apparent translucent area (at base of inner spathe surface); Amazonian Peru, Venezuela, and Brazil ..... 1. *D. amazonense* G. Zhu & Croat

7b. Spathe usually more than 15 cm long, slightly arching toward apex (by up to 45°); with a translucent area (at base of inner spathe surface) 0.5–1 cm high; known from Brazil (Amazonas and Roraima) ..... 19. *D. prancei* G. Zhu & Croat

6b. Inner surface of spathe semiglossy to velvety, obscured with translucent scales.

8a. Seeds reniform, laterally concave, with small cells along dorsal ridge; endemic to Goiás and adjacent areas in Mato Grosso do Sul and Pará, Brazil ..... 5. *D. bogneri* G. Zhu & Croat

8b. Seeds rounded, laterally convex, smooth along dorsal ridge; ranges from Acre, Brazil, to Pando, Bolivia ..... 23. *D. ulei* K. Krause

4b. Spadix visible from face view externally at anthesis; spathe margins slightly to hardly overlapping at the base; French Guiana, Suriname, Guyana, Brazil, and Amazonian Venezuela ..... 18. *D. polyphyllum* L.

3b. Spathe not cymbiform, constricted in lower ⅓ to ½ and differentiated into a proximal tube and a distal lamina; spadix often with one to several appendages (elongated and enlarged tepals) at apex.

9a. Inner surface of spathe never with translucent scales.

10a. Seeds with 5 or 6 thin, strongly discontinuous ridges to 1.5–2 mm high; tropical wet forests, Darién, Panama, to Chocó, Colombia ..... 10. *D. grayumianum* G. Zhu & Croat

10b. Seeds with 3 thick, continuous ridges to 0.5 mm high; tropical moist forests, southern Mexico to central Panama ..... 21. *D. soconuscum* Matuda

9b. Inner surface of spathe densely covered with translucent scales.

11a. Seeds with 4 or 5 thin, slightly interrupted ridges to 1.5 mm high; Guyana, Venezuela, Brazil ..... 7. *D. dubium* Kunth

11b. Seeds with 3 continuous ridges to 0.5 mm high; Caribbean coast of Colombia, and Zulia, Venezuela ..... 20. *D. purdieanum* (Schott) Engl.

2b. Peduncle 30–250 cm above ground level; longest bracteole confined to base of peduncle, never reaching the spathe.

12a. Peduncle 30–90 cm above ground level, less than half as long as petiole.

13a. Spathe apex caudate, 3 to 5 times longer than the body of the spathe; berries apically apiculate; endemic to Loreto and Napo, Peru ..... 2. *D. angustispathum* G. Zhu & Croat

13b. Spathe apex obtuse or acuminate, much shorter than the body of the spathe; berries truncate to subtruncate apically; Central America, French Guiana, or South America as far south as Brazil, but not in Peru.

14a. Spathe 58–78 cm long, 13–21 cm wide, obtuse at apex; seeds reddish brown, 1–1.2 cm diam., with three dorsal ridges; Atlantic slopes of Nicaragua and Costa Rica ..... 8. *D. gigas* (Seem.) Engl.

14b. Spathe 9–20 cm long, 3–5 cm wide, acuminate at apex; seeds light brown, 0.5–0.7 cm diam., with 1 dorsal ridge; Dominican Republic, Puerto Rico, Trinidad, Tobago, Guyana, Surinam, French Guiana, Venezuela, and Brazil.

15a. Spathe 9–10 cm long, acuminate at apex, slightly arching apically up to 45° angle; seeds laterally convex, with many fine pits flanking on both sides of the ridges; French Guiana, near Brazilian border ..... 11. *D. guianense* G. Zhu & Croat

15b. Spathe 10–20 cm long, often arching apically by 45°–90° angle; seeds laterally concave, with coarse, wart-like protuberences flanking the margins on both sides of the ridges; Dominican Republic, Puerto Rico, Trinidad, Tobago, Guyana, Surinam, Venezuela, and Brazil ..... 4. *D. asperum* K. Koch

12b. Peduncle 100–250 cm above ground level, usually more than half as long as petiole.

16a. Spathe cymbiform, never differentiated into a proximal tube and distal lamina.

17a. Spathe obtuse at apex, widest in upper half.

18a. Seeds rounded, the dorsal ridges 4 or 5, strongly interrupted; spathe green externally, the margins broadly overlapping; spadix hidden at anthesis; endemic to the western slopes of the Andes in Ecuador ..... 6. *D. croatii* G. Zhu

18b. Seeds reniform, dorsal ridge 1, continuous; spathe maroon externally, the margins scarcely overlapping; spadix exposed at anthesis; endemic to the Pacific slopes of Costa Rica ..... 16. *D. pittieri* Engl.

17b. Spathe acuminate at apex, widest in lower half.

19a. Spadix 23–35 cm long in fruit; petiole 2–6 m long; seeds rounded, with 3 strong, continuous ridges to 2 mm high; Amazonian Peru and Brazil ..... 15. *D. peruvianum* G. Zhu & Croat

19b. Spadix 4–5 cm long in fruit; petiole 1–2 m long; seeds reniform, with 3 weak continuous ridges to 0.5 mm high; endemic to Acre, Brazil ..... 12. *D. longipes* Engl.

16b. Spathe usually not cymbiform, constricted near the base to yield a proximal tube and distal lamina.

20a. Seeds 0.4–0.6 cm diam., laterally convex, with 1 dorsal ridge; spathe usually wrinkled or lobed along the margins; endemic to southern Peru ..... 17. *D. plowmanii* G. Zhu & Croat

20b. Seeds 0.7–1 cm diam., laterally concave, with 3 dorsal ridges; spathe never wrinkled or lobed along the margins; Colombia, Ecuador, Peru, Brazil, and Surinam.

21a. Inner surface of spathe semiglossy or velvety, densely covered with translucent scales; Colombia, Ecuador, and Peru ..... 3. *D. asperispathum* G. Zhu & Croat

21b. Inner surface of spathe semiglossy or velvety, lacking scales.

22a. Spathe 45–50 cm long, 10–15 cm wide, abruptly acuminate apically; Amazonian Ecuador ..... 9. *D. grandispathum* G. Zhu & Croat

22b. Spathe 20–35 cm long, 3–6 cm wide, gradually acuminate apically; southern Costa Rica to the Pacific slope of Colombia and Ecuador and in the Amazon basin in southern Venezuela, Colombia, Ecuador, Peru, and Brazil (also in Surinam) ..... 22. *D. spruceanum* (Schott) G. Zhu

1. Dracontium amazonense G. Zhu & Croat, sp. nov. TYPE: Peru. Loreto: Iquitos, Altura de Picuruyacu, near confluence of Río Nanay & Río Amazonas, 3°40′S, 73°13′W, 28 Dec. 1979, *C. Davidson & J. Jones 9605* (holotype, MO!; isotype, RSA!). Figures 3A, 4.

Herba usque plus quam 2 m alta; petiolus 1.3–2 m longus; pedunculus subterraneanus, 0–2 cm longus; spatha 10–13 cm longa, 3–4.5 cm lata; extus purpurea; intus velutina, purpurea; spadix 2.5–4 cm longus, 0.8–1.2 cm diam.; baccae globosae, 0.5–0.7 cm diam.; semina rubra, suffusa aurantiaca, usque 0.6 cm diam.

Tuber hemispherical, 8–12 cm diam., 6–8 cm thick, flat above, rounded and white to brown below, 10–20 cm below ground level; tubercles abundant, cylindrically elongated or rounded, 0.5–1 cm diam., 0.8–2 cm long, borne around the periphery of tuber; roots whitish, 1–3 mm diam.; *cataphylls* 2 or 3, 5–22 cm long, 3–5 cm wide, pink-tinged or light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1.3–2 m long above ground, 2.5–4 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth

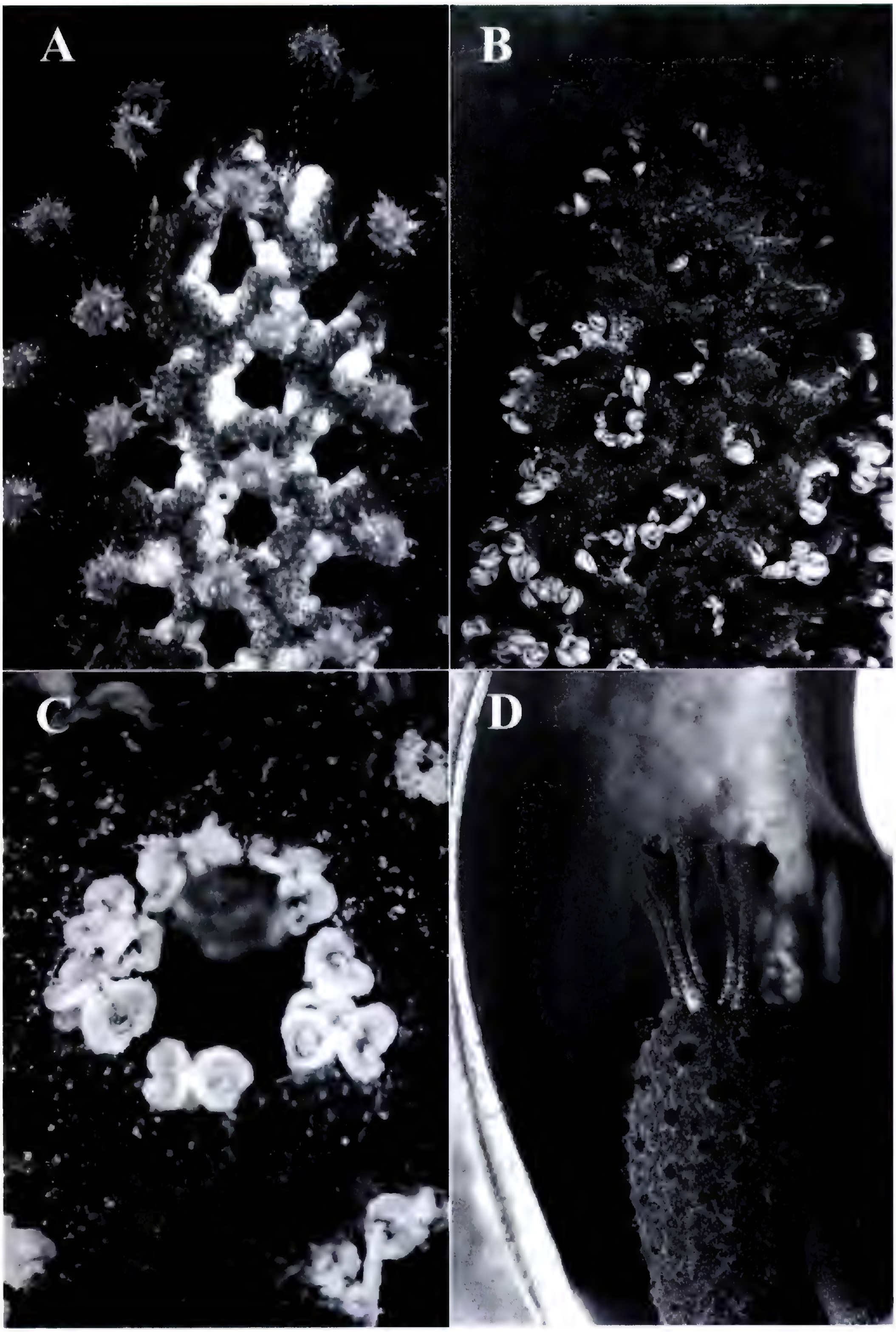

Figure 3. A–D. Flowers. —A. *Dracontium amazonense* (*Croat 56898*). Spadix with protruding stigmas. —B. *D. polyphyllum* (*Croat 74210*). Apex of spadix showing short styles and stamens. —C. *D. spruceanum* (*G. Zhu 1486*). Close-up of flower showing weakly protruding style and a ring of stamens. —D. *D. soconuscum* (*G. Zhu 1502*). Spadix with a cluster of appendages at apex.

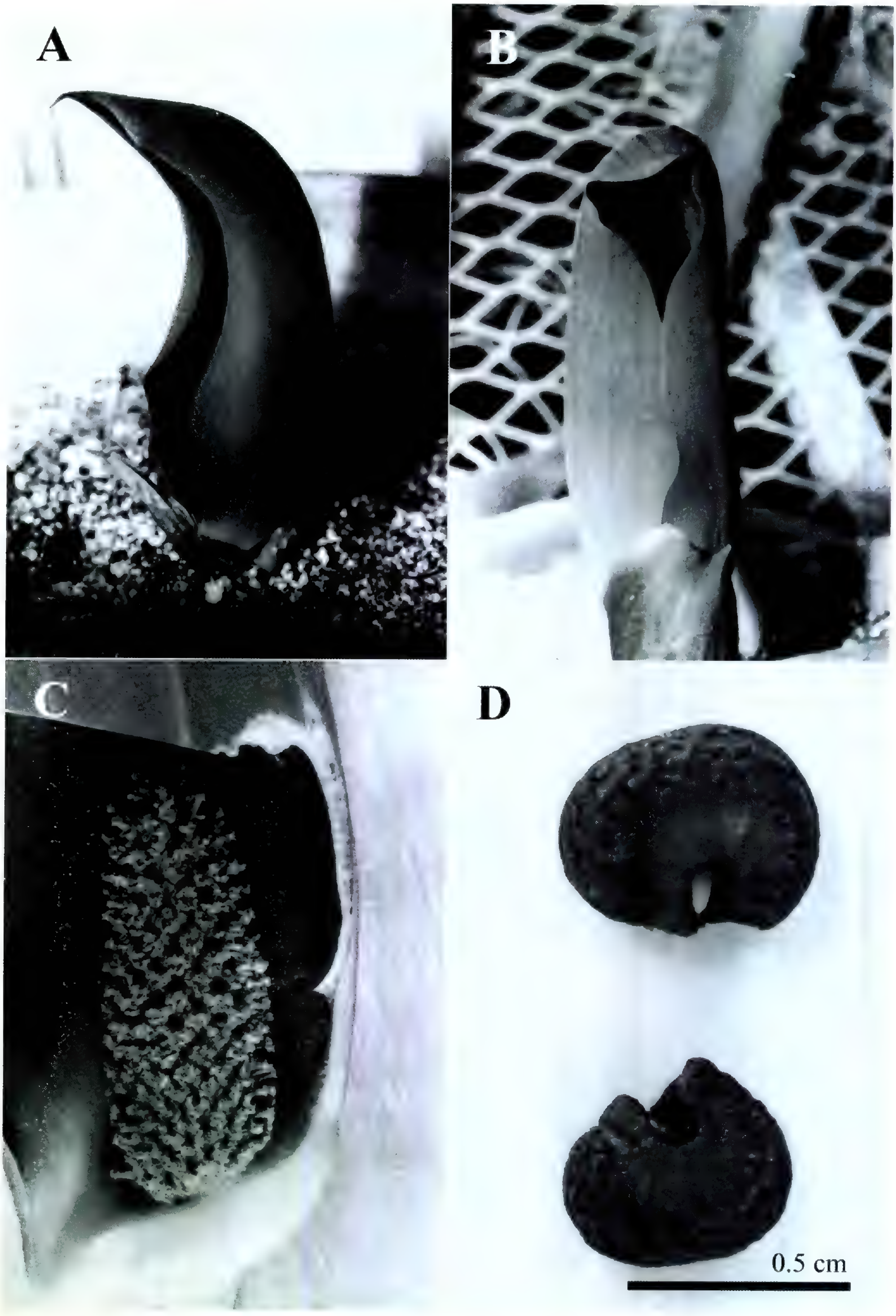

Figure 4. A–D. *Dracontium amazonense*.—A. (*Croat 56898*). Spathe showing side view. —B. (*Croat 71895*). Spathe showing front view. —C. (*Croat 65898*). Spathe with cut-away view showing spadix at anthesis. —D. (*Davidse & Jones 9605*). Seeds in side view.

in upper half and with irregular protuberances in lower half; juvenile blades sagittate, or sagittately lobed; mature *blades* spreading horizontally, 1–1.2 m diam., subcoriaceous, rarely fenestrate, never variegated, often without raphide cells or dark markings, glossy and dark green above, semiglossy and medium green below; *middle division* once or twice trichotomously branched, 45–60 × 40–45 cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 40–55 × 40–50 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, narrowly elliptic, at least some of the basal segments free from each other, often without contrastingly smaller rounded or triangular segments; apices acuminate; *ultimate segments* 10–15 cm long, often confluent with penultimate segments; other segments 7–13 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and weakly raised below; *bracteoles* 1 or 2, 6–22 × 1–2.5 cm, pink tinged, the longest one longer than the peduncle, covering up to ⅓ of the spathe. *Inflorescence* solitary or two, appearing before new leaf; *peduncle* 0–2 cm long above ground, 1–1.2 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, whitish tinged pink, smooth; *spathe* (6–)10–13 × 3–4.5 cm, cymbiform, cucullate, often arching 90°, apex acuminate; inner surface velvety, violet-purple, with translucent area obvious, 0.5–1.5 cm high, shorter than spadix; outer surface maroon, tinged green, matte; margins entire, slightly overlapping at the base; veins obscure inside, conspicuously darker or paler than the spathe, brown; *spadix* often hidden, sessile, cylindric, narrower at apex, brownish purple, 2.5–4 × 0.8–1.2 cm at anthesis, never with appendages at apex; flower tepals 4 to 5, 1.5–2 × 1–2 mm, light brown or brownish purple; stamens 6 to 8; filaments 1–2 mm long; anthers 0.5 mm long, completely exserted; ovary 3-locular, white; stigma unlobed, or 3-lobed; style 0.5–2 mm long above tepals, brownish purple, persistent. *Infructescence* with spadix 3.5 cm long, 1.5 cm diam. in fruit; *berries* 0.5–0.7 × 0.6 cm, globose, apically rounded; young berries pale green; mature berries with abundant raphide cells; *seeds* 0.5–0.6 cm diam., reniform, light brown, laterally depressed; dorsal ridges evident, 3, ± continuous, more than 1 mm thick, warty along both sides, appearing as strongly reduced lateral ridges. Chromosome number $2n = 26$ (*G. Zhu 1454*).

Phenology. Flowering known only in March; mature fruits known only in December.

Distribution and habitat. *Dracontium amazonense* is known from Amazonian Venezuela (Bolívar), Brazil (Amazonas and Pará), and Peru (Loreto). It occurs in the *Tropical moist forest* (T-mf) life zone, at elevations of 60 to 100 m.

Discussion. *Dracontium amazonense* is easily confused with *D. polyphyllum* in both sterile and fertile condition. Mature leaves of both species closely resemble one another, and their inflorescences are superficially similar. However, *D. amazonense* differs in its laterally concave seeds (vs. laterally convex in *D. polyphyllum*) and the spathe usually arching 90° apically (vs. arching 45° in *D. polyphyllum*), as well as by its usually hidden spadix (vs. exposed in *D. polyphyllum*).

A tuber of the type collection (*Davidson & Jones 9605*) of *D. amazonense* was sent to the Missouri Botanical Garden in December 1979. The plant bloomed the following spring, and a fertile specimen (*Croat s.n.*, MO 4369881) was prepared in April 1980. Two years later, two more tubers of this species were brought into cultivation at the Missouri Botanical Garden from Manaus, Amazonas, Brazil (*Croat 53561*, June 1982). However, when we started to study the genus *Dracontium* 10 years later in 1992, both *Davidson & Jones 9605* and *Croat 53561* were missing from the greenhouse. Instead, *D. amazonense* was represented by two other numbers, *Croat 56898* and *Croat & Grayum 59844*, in the greenhouse, each with several mature plants. These plants must have been mislabeled, since both numbers apparently originated from Costa Rica, where *D. amazonense* is unknown. *Croat 56898* was collected by Helen Young from La Selva, in the province of Heredia, where only *D. gigas* occurs. *Croat & Grayum 59844* was collected from the Osa Peninsula, where only *D. pittieri* is known. Therefore, the cultivated plants labeled as *Croat 56898* and *Croat & Grayum 59844* in the Missouri Botanical Garden greenhouse probably originated from the collections *Davidson & Jones 9605* and *Croat 53561* and represent *D. amazonense*.

Dracontium amazonense is one of the most easily grown species in the genus. It blooms regularly and propagates easily in the greenhouse by means of tubercles. However, to the authors' knowledge it had never produced fruit by means of either self-

or cross-pollination. This species has been widely distributed by the Missouri Botanical Garden, under the number *Croat 56898* and the name *D. gigas*, to many institutions worldwide and private aroid growers in the United States.

Paratypes. BRAZIL. **Amazonas:** Manaus, Chacaras de Tarumn, ca. 16 km NW of Manaus, *T. Croat 53561, 56898* (MO); Tefé, Lago Tefé, NW shore, *T. Plowman et al. 12510* (MG, MO); mouth of Rio Bauana, *T. Plowman et al. 12550* (MG, MO, NY). **Pará:** Rio Juruá, Bom Fim, *Ule 5286* (MG). PERU. **Loreto:** Quebrada Yanamono, Explorama Tourist Lodge, Río Amazonas, *P. Maas et al. 8299* (U). VENEZUELA. **Bolívar:** Santa Elena de Uairén, Gran Sabana, campos del Sr. Fernández Peña, *Tamayo 3188* (F, US, VEN).

Cultivated plants. Peru. Loreto: Altura de Pecuruyacu, TYPE: *Davidson & Jones 9605*, (MO 4369881), cult. at Missouri Botanical Garden (MBG) [represented by *G. Zhu 1454, 1456, 1457, 1460, 1461, 1464, 1465, 1489, 1514, 1516* (MO)]. Brazil. Amazonas: Manuas, *T. B. Croat 53561* (MO), cult. at MBG. Ecuador. Napo: Puyo, C. McDaniel s.n., *T. B. Croat 71895* (MO), cult. at MBG.

2. Dracontium angustispathum G. Zhu & Croat, sp. nov. TYPE: Peru. Loreto: Mishuyacu, near Iquitos, 100 m, in forest, *G. Klug 254* (holotype, US!; isotypes, F!, NY!). Figure 5.

Herba usque plus quam 2 m alta; petiolus 1–2 m longus; lamina 35–55 cm longa, 25–35 cm lata; pedunculus 45–65 cm longus, 0.5–1.5 cm diam.; spatha 6–10 cm longa, 1.5–2 cm lata, convoluta basi, apice 20–50 cm longa; extus impolita, sordide purpurea; intus purpurea; spadix 2–5 cm longus, 0.5–1 cm diam.; tepala 5–7; semina brunneola, 0.5–0.65 cm longus, 0.4–0.5 cm lata.

Tuber hemispherical, 6–10 cm diam., 5–6 cm thick, flat above, rounded and white to brown below, 10–15 cm below ground level; tubercles abundant, rounded or cylindrically elongated, 0.5–1 cm diam., 0.6–1 cm long, borne around the periphery of tuber; *cataphylls* 2 or 3, 2–15 cm long, 1–2.5 cm wide, light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–2 m long above ground, 1.5–3.5 cm diam. at midpoint, dark green or brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blades* spreading horizontally, 1–1.2 m diam., thinly coriaceous, rarely fenestrate (sometimes fenestrate in juvenile leaves), never variegated, without raphide cells or dark markings, semiglossy and medium green above, matte and medium green below; *middle division* once or twice trichotomously branched, 35–55 × 25–35 cm, with terminal subdivision consisting of three sections, with each basal subdivision often consisting of an entire segment; lateral divisions twice dichotomously branched, 35–55 × 25–35 cm, with terminal subdivision often consisting of an entire segment, with basal subdivision often consisting of an entire segment; terminal and subterminal sections free, each usually consisting of a single segment; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, lanceolate, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments; apices caudate; *ultimate segments* 20–35 cm long; basal segments absent; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins prominent above, or weakly raised below; *bracteoles* 2 or 3, 5–20 cm long, 1–2 cm wide, dark brown or light brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. *Inflorescence* solitary, appearing before or after new leaf: *peduncle* (35–)45–65 cm long above ground, 0.5–1.5 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, dark green, smooth in upper half; *spathe* 6–10 × 1.5–2 cm, cymbiform, non-cucullate, erect or slightly arching, apex caudate, 3 to 5 times longer than the remainder of the spathe; inner surface semiglossy, maroon, with translucent area obscure (to 3 mm height); outer surface dark purple, matte; margins entire, broadly overlapping or convolute in the lower two-thirds; veins obscure inside and outside, similar to the spathe in color; *spadix* hidden, sessile, cylindric, light brown or purple, 2–5 cm long, 0.5–1 cm diam. at anthesis. Flower tepals 5 to 7, 1.5–2 × 1–1.5 mm, pale green; stamens 6 or 7; filaments 1.5–2 mm long; anthers 0.5–1 mm long, slightly exserted; ovary bilocular, pale green; stigma unlobed, or 2-lobed; style 1–2 mm long above tepals, green, persistent. *Infructescence* with spadix 6–9 cm long, 1.5–2 cm diam. in fruit; *berries* 1.1–1.8 cm diam., 0.8–1 cm thick, obliquely obovoid, apically apiculate; young berry medium green; mature berry orange, with abundant raphide cells; *seeds* solitary, 0.5–0.65 × 0.4–0.5 cm, rounded or reniform, light brown, laterally flattened; dorsal ridges obscure.

Phenology. Flowering from July to April; mature fruits from August to April.

Distribution and habitat. Dracontium angustispathum is found in Loreto Department in Peru, and there is also one collection from Vaupés in Colombia. It occurs in *Tropical moist forest* (T-mf) and *Tropical wet forest* (T-wf) life zones (Holdridge et al., 1971), often in swampy areas, at elevations of 100 to 180 m.

Local names. "Anakaho" (*King 416*, F); "jer-

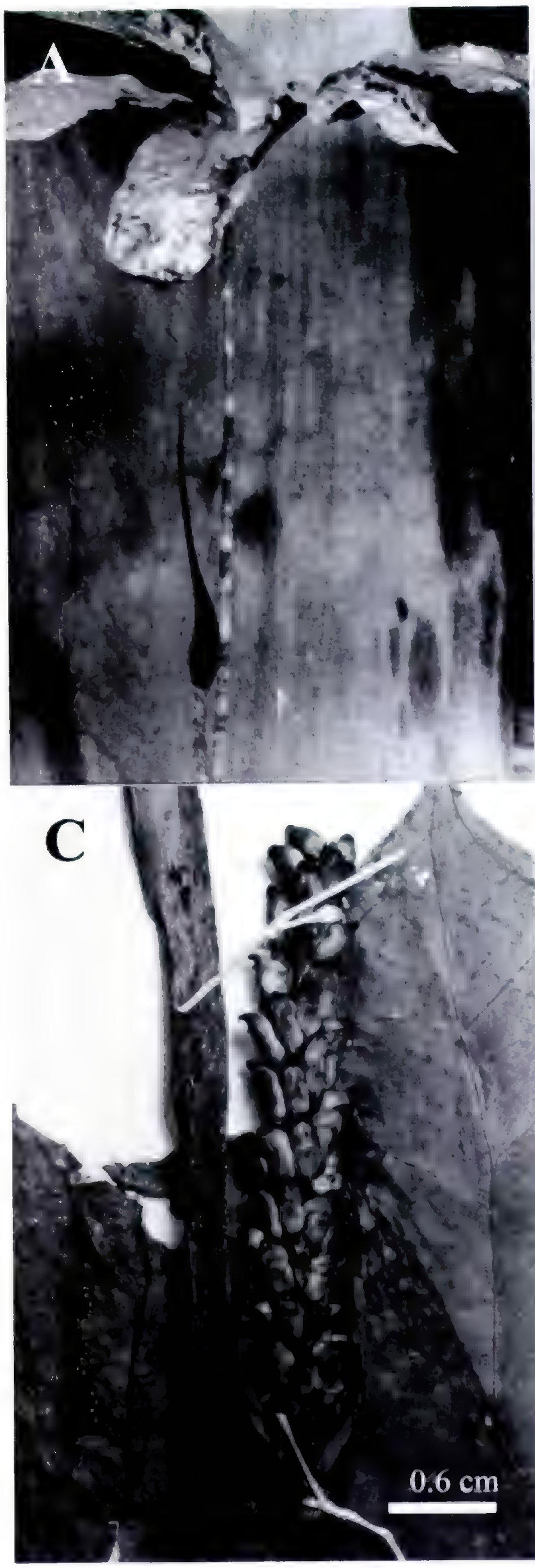

Figure 5. A—D. *Dracontium angustispathum*. — A. Cultivated plant by John Banta, originally collected in Peru in 1986 by Josef Bogner. —B. Specimen showing inflorescence, portions of petiole, and tuber (*Plowman et al. 6720*, GH). —C. Herbarium specimen showing close-up of infructescence (*Stein 3999*). —D. Seeds showing dorsal view (top) and side view (bottom) (*Vásquez et al. 8081*).

gón sacha del bajo" (*Martin & Lau-Cam 1315*, ECON).

Discussion. *Dracontium angustispathum* does not resemble any other member of the genus. It is characterized by its thin spathe less than 2 cm wide at anthesis, with a caudate apex 3 to 5 times longer than the body of the spathe (hence its epithet), leaf-blade divisions usually consisting of a few (3 to 5) segments; and usually 1-seeded berries apiculate apically. This species has been previously identified as the partially sympatric *D. loretense* [*D. spruceanum*], which has a much longer peduncle. Cultivated plants of *D. angustispathum* are only known from John Banta's nursery in Florida.

The new species *Dracontium angustispathum* was previously noted (as nomen nudum) to occur in Peru (Vásquez et al., 2002 [2003]).

Paratypes. COLOMBIA. **Vaupés:** Río Apaporis, at mouth of Río Pacoa, *Schultes 14799* (GH). PERU. **Loreto:** Maynas, Pebas on Río Ampiyacu, *Plowman et al. 6720* (GH); Iquitos, Alpahuayo, Esta. Exp. Inst. Inv. IIAP, Quebrada Brashico, *Vásquez et al. 16524* (MO); Almendras, *Vásquez & Jaramillo 4938* (MO), *7595* (MO); Iquitos, Mishuyacu, *Inchaustegui s.n.* (MO), *Williams 3756* (F); Maynas, Pebas, Bora Native community of Brillo Nuevo, *Plowman et al. 6815* (GH), *Treacy & Alcorn 198* (F); Río Ampiyacu, Bora Pucaurquillo, Ramon Castilla, *Hahn et al. 17* (MO), *Stein 3999* (MO); Río Nanay, Casería Mishana, 30 km SW of Iquitos, Callicebus Biological Reserve, *Foster 4389* (F); Pinto-Cocha, *Williams 827* (F); Puerto Almendras, *Vásquez et al. 8081* (MO). Napo: Río Napo, Negro Urco, *Martin & Lau-Cam 1315* (ECON); Río Santa María, trail E of Secoya, village of "Vencedor," *King 416* (F); Río Blanco, Est. Biol., *Vásquez et al. 6761* (MO); Río Itaya, San Antonio, *Killip & Smith 29351* (NY, US); Río Yubineto, tributary of Río Putumayo, Bellavista Paujilillo, *Haxaire 1757* (MO).

Cultivated plants. Peru. Unknown original locality, *J. Bogner s.n.* (M), cult. in United States, Florida, Alva, John Banta's Nursery, E. Spear; Loreto, Río Sucusari, collected by van der Werff, vouchered, 1 Nov. 1996, *Croat 79428* (MO).

3. Dracontium asperispathum G. Zhu & Croat, sp. nov. TYPE: Peru. Loreto: Maynas, Pebas on Río Ampiyacu, 3°10′S, 71°49′W, 10 Apr. 1977, *T. Plowman, R. E. Schultes & O. Tovar 6729* (holotype, F-1825130!; isotypes, F-1823999!, GH!). Figure 6.

Petiolus 1–2.5 m longus; lamina 50–65 cm longa, 50–60 cm lata; pedunculus 1–1.45 m longus, 1–2.5 cm diam.; spatha 28–46 cm longa, 4–6 cm lata, cucullata basi; extus impolita, sordide viridis; intus velutina, purpurea; spadix 3.5–6 cm longus, 0.7–1 cm diam.; tepala (4–)5–6(–7); semina rubra, 0.6–0.8 cm diam.

Tuber hemispherical, 5–15 cm diam., 4–8 cm thick, flat or slightly sunken above, rounded and white to brown below, 5–20 cm below ground level. Tubercles few, rounded, 0.8–1 cm diam., borne around the periphery of tuber; roots 2.5–3 mm diam.; *cataphylls* 1 to 3, 6–22 × 1.5–3 cm, pinkish or light brown, reaching or surpassing ground level. Leaves solitary; *petioles* 1–2.5 m long, 2.5–4 cm diam. at midpoint, dark green or medium green tinged brown, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth or sometimes with spiny projections; juvenile blade sagittate, or sagittately lobed; mature *blades* spreading horizontally, 1–1.4 m diam., subcoriaceous, sometimes fenestrate, never variegated, without raphide cells or dark markings, semiglossy and dark green above, matte and medium green below; *middle division* twice trichotomously branched, 50–65 × 50–60 cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 47–60 × 45–55 cm, with terminal subdivision consisting of two sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each usually consisting of a single segment or each consisting of a few segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate-oblong or elliptic or lanceolate, mostly free from each other in each division, often without contrastingly smaller rounded or triangular segments; apices acuminate, or rarely acute; *ultimate segments* 20–32 cm long, free from penultimate segments; other segments 9–20 cm long; penultimate segments free from subterminal sections; medial segments often free from basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins prominent above and weakly raised below; *bracteoles* 1 to 4, 4–24 cm long, 1.5–3 cm wide, light brown, the longest one much shorter than the peduncle, confined to the base. *Inflorescence* solitary, appearing before or after new leaf; *peduncle* (56–)100–145 cm long above ground, 1–2.5 cm diam. at midpoint, more than half as long as the petiole or sometimes as long as or longer than the petiole, mottled similar to petiole but deeper in color, dark green, smooth in upper half or with irregular protuberances in lower half or spiny projections; *spathe* 28–46 cm long, 4–6 cm wide, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), erect or slightly arching, apex acuminate; 8–12 cm long, 4–6 cm wide at widest point; lamina 3 to 5 times longer than the tube; inner surface covered with dense, translucent scales 1–2 mm long, olive-brown or red-purple, with translucent area obvious, 8–15 cm high, 1.5–3 times longer than spadix; outer surface green or green tinged

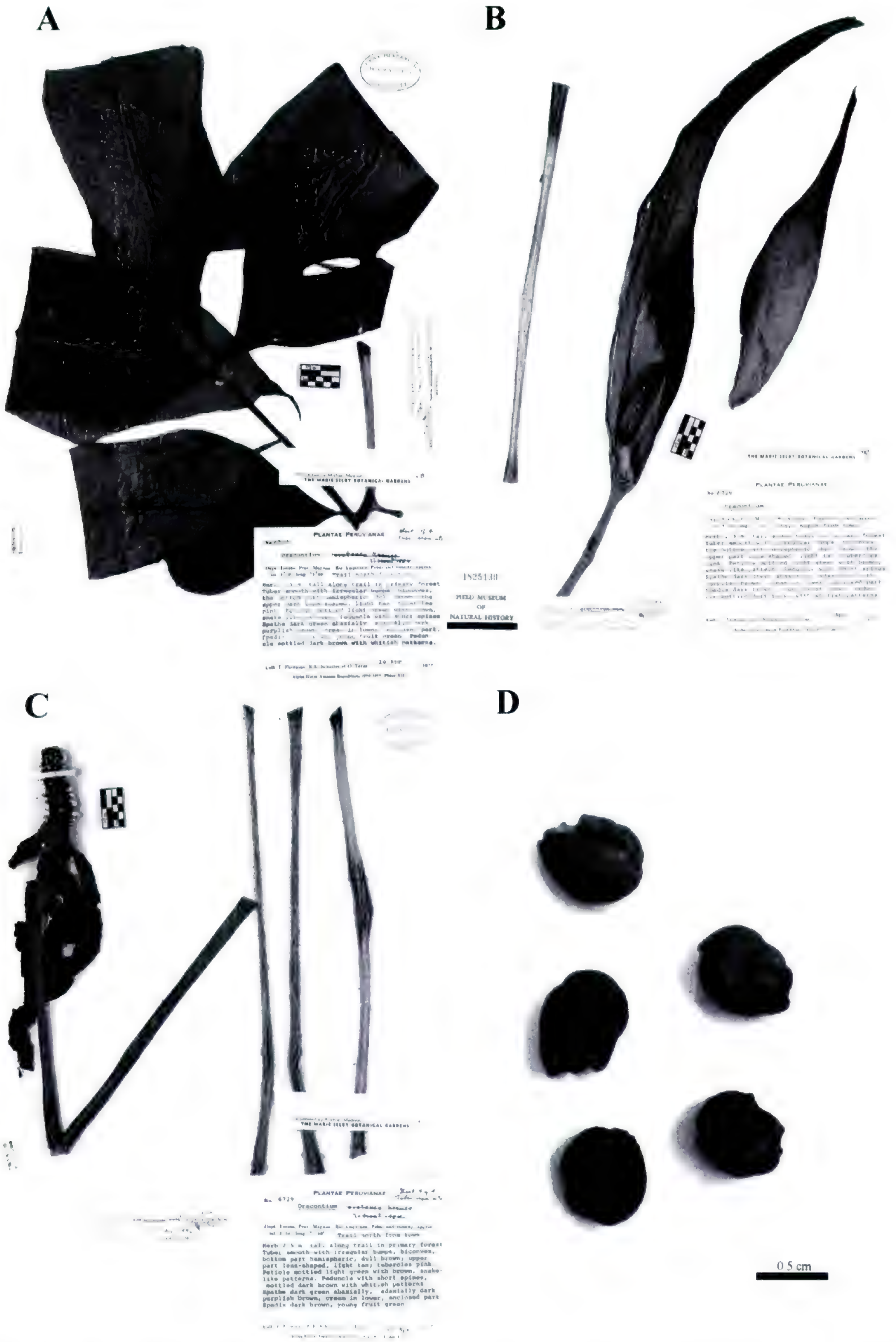

Figure 6. A–D, *Dracontium asperispathum* (*Plowman et al. 6729*). —A. Herbarium type specimen. —B. Herbarium type specimen showing inflorescence. —C. Herbarium type specimen showing infructescence. —D. Seeds in side view.

brown, matte; margins entire, broadly overlapping at the base; veins obscure inside and raised outside, similar to the spathe in color; *spadix* hidden, stipitate, cylindric, brown or purple or dark purple, 3.5–6 × 0.7–1 cm at anthesis, never with appendages at apex; stipe 0.5–1 × 0.5–0.8 cm at anthesis, light brown; flower tepals (4)5 or 6(7), 0.5–2.5 × 1–2 mm, purple or dark purple; stamens 5 to 7; filaments 0.3–2 mm long; anthers 0.3–0.5 mm long, hidden or slightly exserted; ovary 3-locular, pale green or white; stigma unlobed; style 0.5–1.5 mm long above tepals, purple or green, persistent. *Infructescence* with spadix 8–16 × 2–4 cm in fruit; *berries* 0.7–0.8 × 0.7–1 cm, 1- or 2-seeded, obliquely obovoid, apically rounded or subtruncate; young berries medium green; mature berry orange, without reddish dots and raphide cells; *seeds* 0.6–0.8 cm diam., rounded, reddish brown, laterally flattened; dorsal ridges obvious, 3, often strongly interrupted, with the central ridge contrastingly raised, more than 1 mm thick, 0.1–0.2 mm high, warty along ridges.

Phenology. Flowering from January to September; mature fruits from April to August.

Distribution and habitat. *Dracontium asperispathum* ranges from the Amacayacu area in Colombia (Amazonas) to Amazonian Ecuador (Napo) and along Río Amazonas and Río Napo in Peru (Loreto). It occurs in *Tropical moist forest* (T-mf) and *Premontane moist forest* (P-mf) life zones (Holdridge et al., 1971), at elevations of 100 to 230 m.

Local name. "Jergón sacha" (*Williams 1942*, F; *Plowman & Martin 1661*, ECON).

Discussion. *Dracontium asperispathum* is easily confused with *D. spruceanum* where their ranges overlap in the upper Amazon basin because they have very similar leaves and a long-pedunculate elongated purplish spathe, but the former differs in having the spathe inner surface covered with dense, translucent scales (hence, the name *asperispathum*).

The new species *Dracontium asperispathum* was previously noted (as nomen nudum) to occur in Peru (Vásquez et al., 2002 [2003]).

Paratypes. COLOMBIA. **Amazonas:** Amacayacu, Par. Nac. Nat. Amacayacu, Trocha de Matamatá, *J. Pipoly 15612* (MO). ECUADOR. **Napo:** Par. Nac. Yasuní, Pozo Petrolero Conoco-Amo 2, *D. Neill et al. 8160* (CM, MO, QCNE). PERU. **Loreto:** Explorama, Napo Camp, Las Amazonas, Quebrada Sucusari, *Gentry et al. 42629* (MO); Explorama Inn, 1 km S of Indiana, Río Amazonas, *Gentry et al. 54686* (MO); Yanamono, *Díaz et al. 1164* (MO); Explorama Camp, Río Amazonas above mouth of Río Napo, *Gentry et al. 29076* (MO); Iquitos, *Maare 189* (ECON); Picurugacu, *Plowman & Martin 1661* (ECON); Río Ampiyacu at Pebas, *Plowman et al. 6728* (F, GH); Río Amazonas at Pebas, *Williams 1750, 1942* (F); Río Amazonas, Caballo-Cocha, *Williams 2119* (F, US); Río Napo, Isla Inayuga, *Croat 20550* (F, MO); Río Yaguasyacu, Brillo Nuevo, *Plowman et al. 6820* (GH); Ushpacaño, near Iquitos, *Tina & Tello 2054* (ECON); Varadero de Mazan from Río Amazonas to Río Napo, *Croat 19391* (MO); Río Itaya, *Williams 155* (F).

4. **Dracontium asperum** K. Koch, Wochenschr. 33: 259. 1859. TYPE: Surinam. Nickerie, 12 km N of Lucie River, 3 km S of Juliana Top, 3°36′–41′N, 56°30′–34′W, 300 m, *H. S. Irwin et al. 55045* (neotype, designated by Zhu & Grayum (1995: 522), NY!; isotypes, COL!, F!, GH!, K!, US!, VEN!). Figure 7.

Dracontium elatum Masters, Gard. Chron. 1: figs. 58, 344. 1870. TYPE: Guyana. Distributed by Linden and in cultivation at Sanders's nursery, *Sanders 1920* (lectotype, designated here, K!).

Dracontium foecundum Hook. f., Bot. Mag. 1885: t. 6808. 1885. TYPE: Guyana. Orealla, Corentyne River, near coast, 5°19′N, 57°20′W, 2 Mar. 1882, *W. W. E. Im Thurn s.n.* [from cultivar] (holotype, K!).

Tuber hemispherical, 4–16 × 3–8 cm, flat or slightly convex above, rounded and whitish to brownish below, 15–35 cm below ground level; tubercles abundant, cylindrically elongated, 0.5–1 × 1–3 cm, borne around the periphery of tuber; roots white, 2–3 mm diam.; *cataphylls* 1 to 3, 14–35 × 2–5.5 cm, pinkish or light brown, reaching or surpassing ground level. Leaves solitary or sometimes 2 or more per tuber; *petioles* 1–2 m long above ground, 2–4 cm diam. at midpoint, gray or whitish green (especially when young) or medium-green-tinged brown, scarcely mottled, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blades* ascending to 45° to the petiole spreading horizontally, 1–1.3 m diam., papyraceous, rarely fenestrate, never variegated, without raphide cells or dark markings, glossy and medium green above, glossy and dark green below; *middle division* twice trichotomously branched, 1–1.2 cm long, 0.9–1.1 cm wide, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, 0.75–0.98 × 0.8–1 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; leaf segments bilobed or irregularly lobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate or oblanceolate, at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices

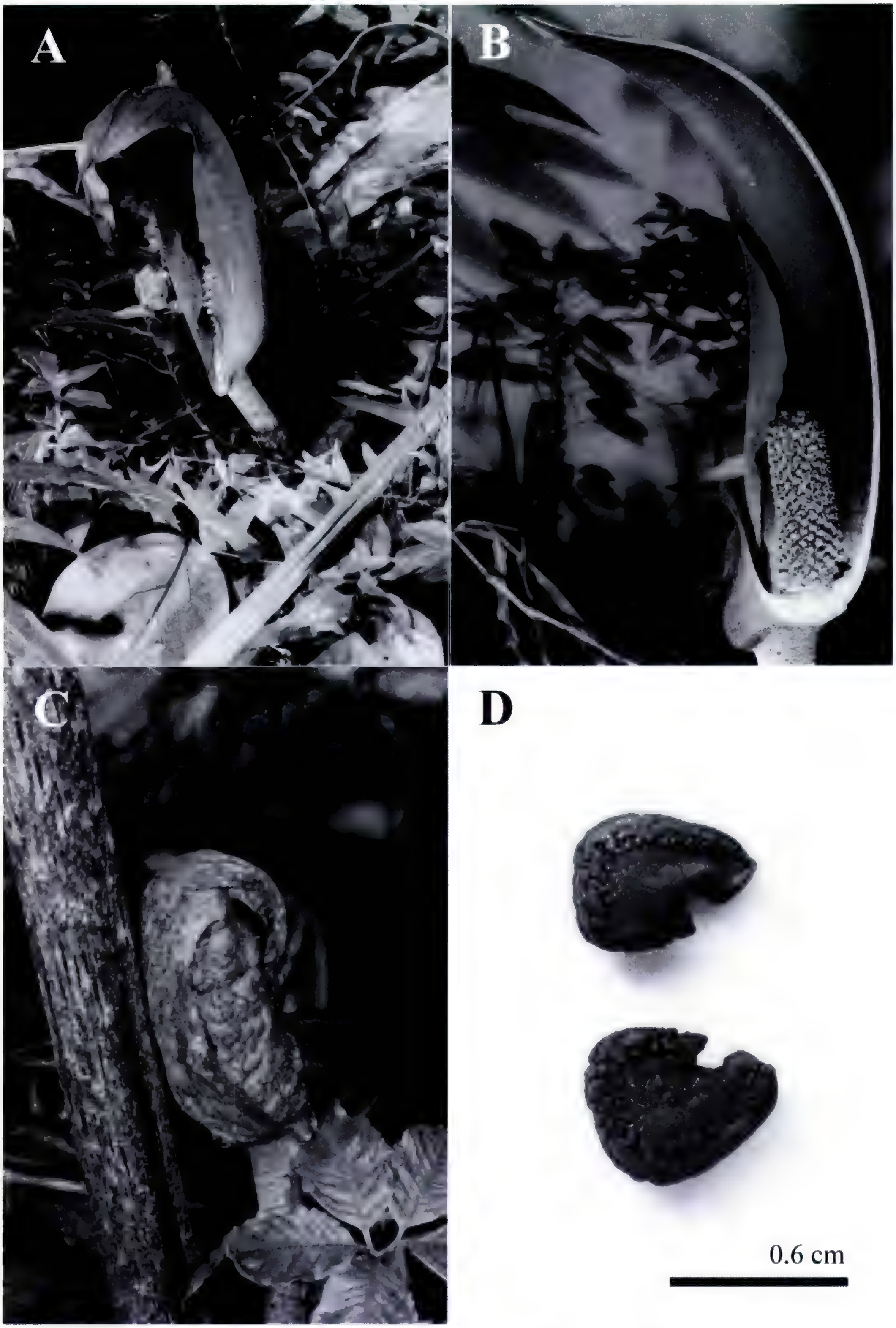

Figure 7. A–D, *Dracontium asperum*. A, B. Photos taken at Orange Grove Estate, Trinidad, by Hans Boos. —A. Inflorescence at anthesis. —B. Inflorescence with one side removed to expose interior of spathe and the spadix at anthesis. —C. (*G. Zhu 1509*). Cultivated plant by Hans Boos in Trinidad showing base of petiole and infructescence with immature fruits and persistent spathe. Photo by Hans Boos. —D. Seeds from Trinidad sent by Julius Boos.

acuminate, or acute (rarely); *ultimate segments* 12–20 cm long, free from penultimate segments; other segments 6–15 cm long; penultimate segments not free from subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, with spiny projections (sometimes); tertiary veins conspicuous above and weakly raised below; *bracteoles* 1 or 2, 4.5–37 × 1.5–3 cm, dark brown mottled with light brown, the longest one much shorter than the peduncle, confined at the base. *Inflorescence* usually solitary, rarely 2, appearing before new leaf; *peduncle* 5–17 cm long above ground, 0.5–0.8 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, brown-green, often with irregular protuberances; *spathe* (10)13–20 × 3–5 cm, cymbiform, cucullate, often arching 45°–90°, apex acuminate; inner surface velvety, maroon or purple-red or red-purple, with the translucent area obvious, 1–2 cm high, shorter than spadix; outer surface maroon, tinged green or dark purple, matte; margins entire, hardly overlapping at the base; veins obscure or obvious inside and outside, similar to the spathe in color, marcescent on developing infructescence; *spadix* exposed, sessile, cylindric, purple, 2.6–4 × 0.8–1.1 cm at anthesis, never with appendages at apex; flower tepals (4 to)5 or 6(to 7), 3–4 mm long, 1–2 mm wide, dark purple; stamens (5)6 or 7; filaments 3–4.5 mm long; anthers 1–1.5 mm long, completely exserted; ovary 3- or 4-locular, pale green; stigma 2- or 3-lobed; style 1–3 mm long above tepals, dark purple, persistent. *Infructescence* with spadix 8–15 × 3–4 cm in fruit; *berries* 0.8–1.2 cm diam., 0.8–1 cm thick, subglobose, 3- to 6-angular, apically subtruncate; young berry light green; mature berry purplish brown, with abundant reddish dots and raphide cells (dried berries); *seeds* 1- to 3-seeded, 0.5–0.7 cm diam., triangular (±) or rounded, light brown, laterally depressed; dorsal ridges obvious, 3, continuous, more than 1 mm thick, warty along both sides, these appearing as another set of strongly reduced lateral ridges. Chromosome number $2n = 26$ (*Bogner 1132*, M; Petersen, 1989).

Phenology. Flowering mainly from January to March, also in December and from June to August; mature fruits from January to August.

Distribution and habitat. *Dracontium asperum* is a widely distributed species in the Guyana highlands from coastal Surinam and adjacent Brazil (Amazonas), throughout Guyana, ranging into the West Indies from the islands of Trinidad, Puerto Rico, and Dominican Republic. It is likely to be found in northeastern Venezuela since it is phytogeographically related to Trinidad. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at elevations of 30 to 330 m. *Dracontium asperum* is also known from Dominica and Martinique (Jo Ann Baptiste & Julius Boos, pers. comm.). Julius Boos (pers. comm.) suggests that some of the distribution of this species in the West Indies is partly the result of its probable distribution by means of its use as a journey food by native peoples moving from island to island.

Discussion. *Dracontium asperum* is distinguished by its often strongly hooded spathe with the margins broadly overlapping in the lower half at anthesis, hidden spadix, peduncle much longer than the longest bracteole 10–35 cm long above ground level, laterally concave seeds with a single strongly interrupted dorsal ridge coarsely ornamented with wart-like structures flanking the ridge, and usually many tubercles at the tuber apex. One of the most perplexing taxonomic problems in the genus *Dracontium* was the confusion involving *D. asperum* and *D. polyphyllum*, resolved by the designation of a neotype for the former and an epitype for the latter (Zhu & Grayum, 1995). *Dracontium asperum* is also similar to *D. prancei*, which differs in having the bracteoles usually longer than the peduncles and covering the base of the spathe.

Dracontium asperum was described by Koch (1859) over a century after *D. polyphyllum* (1753), from a plant introduced from Surinam and cultivated at the Berlin Botanical Garden that had been obtained from the Botanical Garden in Amsterdam. The holotype of *D. asperum* prepared by Koch and presumably deposited at B was either destroyed or lost.

Dracontium polyphyllum differs from *D. asperum* in having a shorter, slightly broader (6–12.5 cm long, 3–5 cm wide), slightly arching spathe (arching < 45° angle) with the margins hardly or slightly overlapping at base at anthesis. The inner surface is violet-purple with a whitish area 0.5 cm high around the spadix at the base. The peduncle is 0–5 cm long above ground level, and the cataphyll is often longer than the peduncle and surpassing the base of the spathe. Berries have 3 seeds that are 0.4–0.7 cm in diameter, convex on both sides with a continuous dorsal ridge. In addition, the tuber usually has only a few tubercles at the apex. The species is known from northern Brazil, French Guiana, and Surinam. In contrast, *D. asperum* differs from *D. polyphyllum* in having a spathe 13–20 cm long, 3–5 cm wide, often arching 45°–90° at the apex and which is strongly hooded with the margins

broadly overlapping in the lower half at anthesis, often completely covering the spadix. The inner surface is purple to purplish red with a whitish area 1–2 cm high at base. The peduncle is 14–45 cm long above the ground and the cataphyll is much shorter than the peduncle, never reaching the base of the spathe. The seeds are 1 to 2 (rarely 3) per berry and 0.5–0.7 cm in diameter and are strongly depressed on both sides with a strongly interrupted dorsal ridge. The tuber often has many tubercles at the apex.

About 10 years after the discovery of *Dracontium asperum*, a plant corresponding to *D. asperum* was redescribed as *D. elatum* by Masters (1870), based on a cultivated specimen from William Bull's horticultural establishment in Chelsea, England. In the protologue, the origin of the plant was mistakenly referred to as tropical West Africa, where this strictly Neotropical genus does not occur. This plant was believed by Masters to have been introduced into England from Guyana by the British. It is very likely that the plant was distributed by J. J. Linden, a plant importer and dealer in Brussels, since a fertile specimen (*Sanders 1920*, K) identified as *D. elatum* was prepared later in 1870 from a plant cultivated at Sanders's nursery and obtained from Linden under the name "*Sauromatum asperum*," a name mistakenly used for *D. asperum*. This collection, *Sanders 1920* (K), is designated here as the lectotype of *D. elatum* because no material exists from the living collections cultivated by Bull and because the specimen is believed to be from the same living plant. Thus, the specimen prepared by Saunders is preferable to the cited figure 58 in the protologue.

Ten years after the discovery of *Dracontium asperum*, another collection of this species was made by W. W. E. Im Thurn at Pomeroonon on the Guyana side of the Corentyne River near the Atlantic Coast and was subsequently redescribed by J. D. Hooker as *D. foecundum* in 1885.

Additional specimens examined. BRAZIL. **Amazonas:** Yanomami, Rio Demini, Watoriketheri, below Serra Demini, *Milliken 1717* (K, MO). DOMINICAN REPUBLIC. **Duarte:** Caño Azul, Villa Rita, *Liogier 19363* (NY). **Essequibo:** Kuyuwini River, 150 mi. from mouth, *Smith 3029* (F, GH, K, NY, U, US). PUERTO RICO. Río Abajo State Forest, ca. 0.7 km due S of Camp Radley, *Proctor 46104* (SJ); SW of Vega, Baja Rd. 155, km 53, *Woodbury s.n.* (NY); San Juan, Barrio Aibonito, Guajataca Rec. area, 0.4–0.9 km SW of Rd. 437 & Rd. 113, *Proctor 46460* (SJ), *G. Zhu 1445*, (MO); Río Tudras, Forest Station, *Britton & Britton 10060* (NY). **Locality unknown:** Demerara River, *Jenman 6895* (NY); *Wullschlägel 1096* (BR). **National District:** El Enjuagodor, *Jimenez 3420* (US). GUYANA. **Sierra de Luquillo:** Barrio Mameyes, 0.9 km due SSE of La Vega, *Proctor 47976* (SJ). SURINAM. **Brokopondo:** 2.4 km S of Gansee, Feroe Creek, *Donselarr 1159* (U). **Commewijne:** *Florschutz & Maas 3162* (NY, U). **Nickerie:** Zuid River, 2 km above mouth of Lucie River, *Irwin et al. 55749* (NY). TRINIDAD & TOBAGO. **Trinidad:** Buenos Aires, Erin, *Broadway 7455* (NY); Cumuto Rd., *Kalloo & Gonzales 1358* (TRIN); Manzanilla to Mayaro Rd. at mi. 25, *Johnson 243* (TRIN); Nestles Milk Factory, *Barnes s.n.* (TRIN 18584); Orange Grove, Churchill Roosevelt Hwy., *Boos s.n.* (TRIN 31296).

Cultivated plants. Guyana: Orealla, left bank of Corentyne River, cult. Royal Botanical Gardens at Kew, Great Britain, *Im Thurn s.n.* (K), *Jenman 491* (K); originally from Leiden Botanical Garden, hort. Saunders, *Saunders 1920* (K). Trinidad: cult. Botanic Gardens of St. Avis, Florida, U.S.A., *Broadway 5212* (F); originally collected at Orange Grove Estates in Trinidad by J. Boos, 1988, cult. at Royal Botanical Gardens at Kew, Great Britain, *G. Zhu 1442, 1444, 1479, 1497, 1515* (MO); collected by H. Boos, Mar. 1993, *G. Zhu 1484* (MO); Port of Spain, collected by H. Boos, *G. Zhu 1509* (MO). Puerto Rico: cult. Washington, D.C., *Barret s.n.* (US).

5. Dracontium bogneri G. Zhu & Croat, sp. nov. TYPE: Brazil. Goiás: Rio Sobrado, bei der Brücke, cultivated at München Botanical Garden, 1994, *J. Bogner 2097* (holotype, MO-04633684!; isotype, MO-04633683!, RJ!). Figure 8.

Petiolus 1–2 m longus; lamina 50–62 cm longa, 40–50 cm lata; pedunculus subterraneanus, 0–1.5 cm longus; spatha 2.9–7.3 cm longa, 1.4–2.8 cm lata; extus brunneola; intus velutina, purpurea; spadix 1.2–2 cm longus, 0.5–0.7 cm diam.; baccae subglobosae, usque 0.8 cm diam.; semina brunneola, usque 0.5–0.6 cm diam.

Tuber hemispherical, 8 cm diam., 5 cm thick, flat or slightly sunken above, rounded and whitish to pinkish below, 25–30 cm below ground level; tubercles few, rounded or obovoid, 0.6–1.2 cm diam., borne around the periphery of tuber; roots 0.3 cm diam., white, sometimes tinged pink near the base; *cataphylls* 1, 24–25 × 2–4 cm, pink, reaching or surpassing ground level. Leaves solitary; *petioles* 1–2 m long above ground, 1.2–2 cm diam. at midpoint, brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually with spiny projections; juvenile blade sagittate, or sagittately lobed; mature *blades* spreading horizontally, 0.5–1 m diam., papyraceous, rarely fenestrate, never variegated, without raphide cells or dark markings, semiglossy and medium green above, semiglossy and medium green below; *middle division* twice trichotomously branched, 50–62 cm long, 40–50 cm wide, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 0.5–0.6 × 0.4–0.5 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and

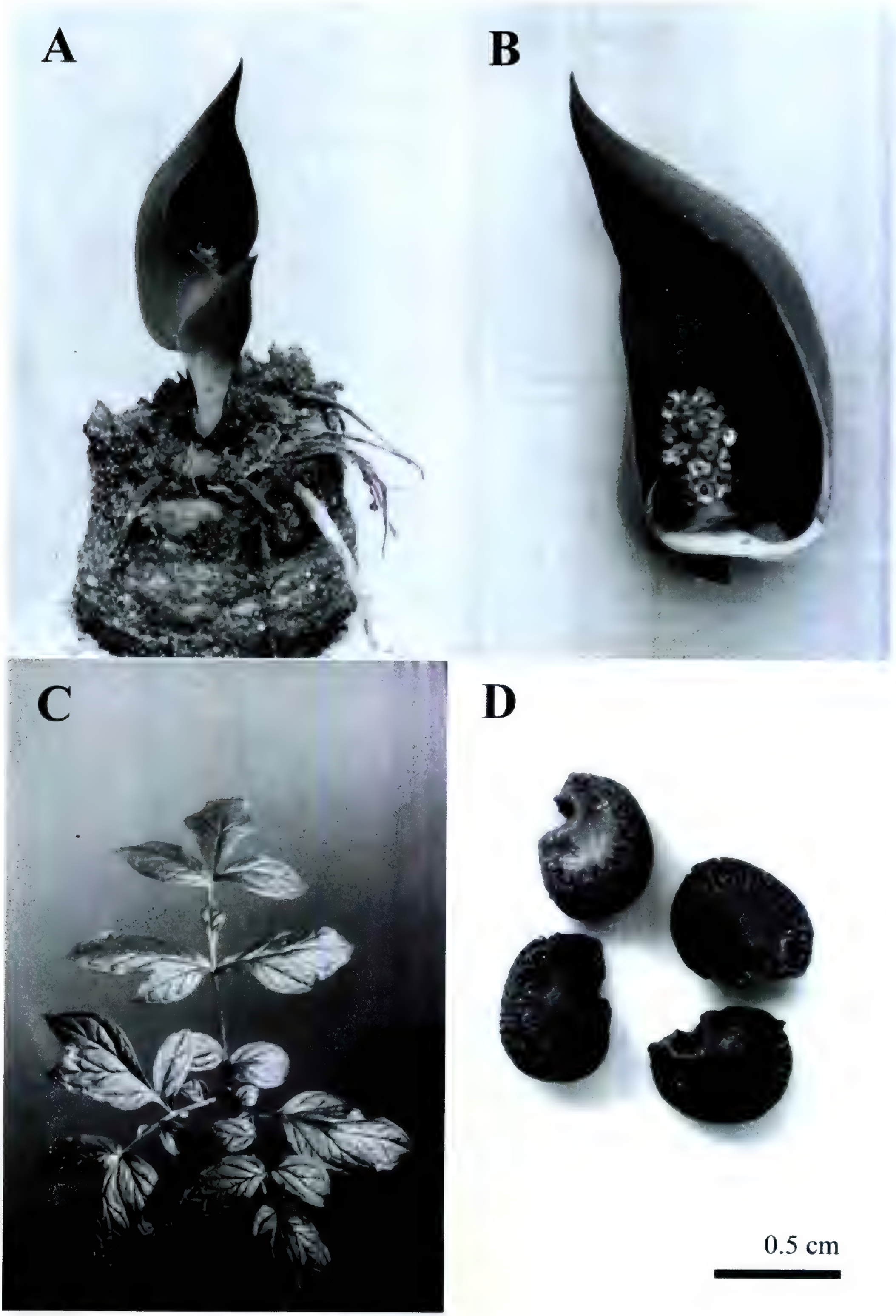

Figure 8. A–D. *Dracontium bogneri*. A–C. Photos by J. Bogner from type, *Bogner 2097*. —A. Flowering plant with tuber and inflorescence. —B. Spathe cut away to expose the interior of the spathe and the spadix at anthesis. —C. Leaf blade. —D. Seeds in side view (*Irwin et al. 34730*).

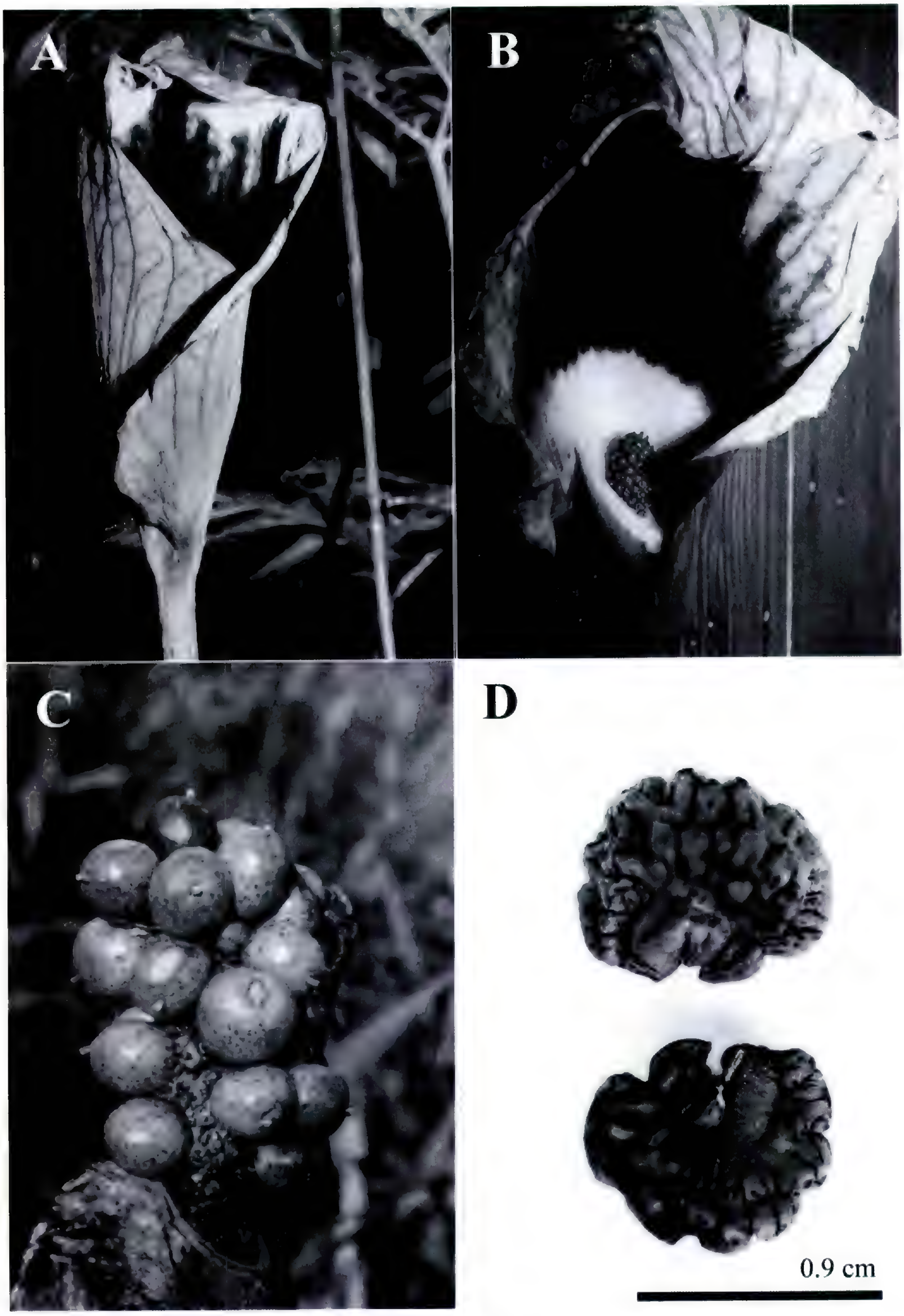

Figure 9. A–D, *Dracontium croatii*. —A. Inflorescence of live type plant voucher at anthesis (*Croat 72368*). —B. Spathe with one side removed to expose interior and spadix at anthesis. —C. Close-up of infructescence. —D. Seeds in side view (from *Dodson & Fallen 7762*).

subterminal sections free, each usually consisting of a single segment; leaf segments often entire or bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate-oblong and lanceolate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or caudate; *ultimate segments* 12–15 cm long, often confluent with penultimate segments; other segments 5–8 cm long; penultimate segments free from subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, tinged brown or similar to petiole but in much paler shades, smooth; tertiary veins prominent above and weakly raised below; bracteole 1, 1.8–6 × 1.2–2.4 cm, dark brown, the longest one longer than the peduncle, covering up to ⅓ of the spathe. *Inflorescence* solitary, appearing before new leaf; *peduncle* 0–1.5 cm long above ground, 0.3–0.6 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, brownish green, smooth; *spathe* 2.0–7.3 cm long, 1.4–2.8 cm wide, cymbiform, cucullate, arching to 45°, apex acuminate; inner surface covered with dense, translucent scales 1–2 mm long, purple-red and olive-brown, with translucent area obscure; outer surface olive-brown, semiglossy or matte; margins entire, broadly overlapping at the base; veins obscure inside and raised outside, conspicuously darker or paler than the spathe, brown; *spadix* exposed (±), stipitate, cylindric, light brown or brown, 1.2–2 × 0.5–0.7 cm at anthesis, never with appendages at apex; stipe 0.2–0.4 × 0.3–0.6 cm at anthesis, light brown or brown. Flower tepals 4 or 5, 1.5–2 mm long, 1 mm wide, light brown; stamens (7)8 or 9; filaments 0.3–3.5 mm long; anthers 0.8–1 mm long, completely exserted; ovary bilocular, pale green; stigma 4-lobed; style 1–1.5 mm long above tepals, greenish, persistent. *Infructescence* with spadix 5.5 × 2.8 cm in fruit; *berries* 4-seeded, 0.8 cm diam., 1 cm thick, subglobose, 3- to 6-angular, apically subtruncate; young berry light green, without reddish dots and raphide cells; mature berry yellowish orange; *seeds* 0.5–0.6 × 0.5–0.6 cm, reniform, light brown, laterally depressed; dorsal ridges obvious, 3, ± continuous, more than 1 mm thick, finely decorated with small cells on both sides.

Phenology. Flowering in November; mature fruits in January.

Distribution and habitat. *Dracontium bogneri* is endemic to Brazil in Goiás and adjacent areas in the states of Mato Grosso do Sul and Pará. It occurs in *Premontane moist forest* (P-mf) and *Tropical montane wet forest* (TM-wf) life zones, at elevations of 300 to 1000 m.

Discussion. *Dracontium bogneri* has the smallest spathes in the genus, as small as 2 cm long and 1.4 cm wide. It is characterized by having a completely subterranean peduncle and the inner spathe surface covered with translucent scales. It is superficially close to *D. ulei* in having an almost completely subterranean peduncle, but that species differs in having laterally convex, smooth seeds (vs. laterally depressed, finely decorated seeds for *D. bogneri*). This species is named in honor of Josef Bogner, of the Munich Botanical Garden, who independently recognized this taxon as an undescribed species at the time that he collected it. He is one of the foremost aroid specialists in the world, whose significant aroid collections from South America include the type specimen of this species.

Paratypes. BRAZIL. **Goiás:** 14 km S of Niquelândia, 14°25′S, 48°20′W, 1000 m, *H. S. Irwin et al. 34730* (NY). **Minas Cerais:** Municipo de Itaberiera, road from Itaberiera to Claudio, then side road to Serranha, 900 m, 8°58′S, 72°47′W, in shade of seasonally dry woods, 2 Feb. 1993, *G. Zhu 1510* (MO) [originally collected, A. Meerow et al.].

Cultivated plants. Brazil. Pará, Conceição do Araguaia, 20 km W of Redenção, cult. by Allen Fernández, South Miami, Florida, U.S.A., *T. Plowman 12043* (F).

6. Dracontium croatii G. Zhu, Novon 5: 301. 1995. TYPE: Ecuador. Lita-San Lorenzo, 15.5 km W of Lita, San Lorenzo Cantón, Esmeraldas, 0°55′N, 78°28′W, 705 m, *G. Zhu 1493* (holotype, MO!). [Originally collected, *T. B. Croat 72368* (MO), cult. at MBG.] Figures 2B, 9.

Tuber hemispherical, 8–11 cm diam., 6.5 cm thick, flat above, rounded and whitish to brownish below, 4–30 cm below ground level; tubercles few, rounded or cylindrically elongated, 0.5–1 cm diam., 1–2.3 cm long, borne around the periphery of tuber; roots whitish, 2–4 mm diam.; *cataphylls* 3 to 5, 5–45 × 3–5 cm, dark brown or pink, 5–15 cm long above ground. Leaves solitary; *petioles* 1.4–3 m long above ground, 2–4.5 cm diam. at midpoint, dark green or brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blades* spreading horizontally, 1–1.5 m diam., thinly coriaceous, rarely fenestrate, never variegated, without raphide cells or dark markings with abundant raphide cells, semiglossy and dark green above to matte and medium green above, semiglos-

sy and medium green below to matte and medium green below; *middle division* twice trichotomously branched, 0.8–1 × 0.5–0.8 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 0.8–0.95 × 0.5–0.8 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly confluent with each other in each division or at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or rarely acute; *ultimate segments* 20 cm long, confluent with penultimate segments; other segments 3.5–15 cm long; penultimate segments confluent with the subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other or rarely confluent with each other; rachises patterned similar to petiole but in much paler shades, with irregular protuberances; tertiary veins prominent and conspicuous above; *bracteoles* 3 or 4, 20 × 2–4 cm, light or dark brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. *Inflorescence* solitary, appearing before new leaf; *peduncle* 80–120 cm long above ground, 1.3–3.5 cm diam. at midpoint, more than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, with irregular protuberances in lower half and spiny projections; *spathe* 23–50 cm long, 8–15 cm wide, cymbiform, cucullate, erect or slightly arching, apex obtuse; inner surface velvety, maroon and solid greenish white (4–6 cm along the margin), with translucent area obvious, 3–7 cm high, 1.5 to 3 times longer than spadix; outer surface dark yellowish green, matte; margins entire, broadly overlapping in the lower two-thirds; veins obscure inside, conspicuously darker or paler than the spathe, purple and pale green (on lower half); *spadix* hidden, sessile, cylindric, narrower at apex, purple, 1.8–6.5 cm long, 0.7–1.5 cm diam. at anthesis, never with appendages at apex. Flower tepals (6)7 or 8(9), 1.8–2.2 × 1–2 mm, brown-purple or dark purple; stamens 6 to 9; filaments 1.5–2 mm long; anthers 1–1.5 mm long, hidden or slightly exserted; ovary bilocular, pale green; stigma 2-lobed, or rarely 3-lobed; style 1–1.2 mm long above tepals, purple, persistent. *Infructescence* with spadix 6–12 cm long, 3.4–5 cm diam. in fruit; *berries* 2-seeded, 1–1.8 cm diam., globose, apically rounded; young berry light green; mature berry orange, with or without some reddish dots or raphide cells; *seeds* 0.8–1 cm diam., rounded, reddish brown, laterally depressed; dorsal ridges obvious, more than 3, strongly interrupted, monomorphic, more than 1 mm thick, 1–2 mm high, smooth on both sides.

Phenology. Flowering from November to February; mature fruits from February to July.

Distribution and habitat. *Dracontium croatii* is known only from the western slopes of the Andes in Ecuador; it may also occur in adjacent areas in Colombia. It occurs in *Premontane wet forest* (P-wf) and *Tropical montane moist forest* (TM-mf) life zones (Holdridge et al., 1971), at elevations of 450 to 1000 m.

Local names. "Papayuëla" (*Barfod 41597*, MO).

Discussion. Morphologically, *D. croatii* does not appear to be particularly close to any member of the genus. It is readily distinguished by its showy greenish spathe that is unique in *Dracontium*, by the matte upper leaf-blade surface (typically semiglossy elsewhere), and globose mature fruits and seeds that are up to 1 cm in diameter, the largest in the genus.

This species was named in honor of Thomas B. Croat of the Missouri Botanical Garden, who served as the chairman for the first author's dissertation committee and laid the foundation of this work through his collections of both herbarium specimens and photographic materials.

Additional specimens examined. ECUADOR. **Carchi:** For. Res., Awá Ethnic Reserve, *Hoover et al. 3279* (QCA); San Marcos-Tobar Donoso, *Barfod 41597* (AAU, MO, QCA). **Pichincha:** bridge over Río Chiguilpe near jct. w Río Baba, 7 km from jct. of entrance rd. at 7 km from Santo Domingo on hwy. to Quevedo, *Dodson 5951* (SEL); La Centinela, at crest of Montañas de Ila on rd. 12 km from Patricia Pilar to 24 de Mayo, *Dodson & Fallen 7762* (MO, QCNE, SEL); La Centinela, 13 km E of Santo Domingo–Quevedo Hwy. in Patricia Pilar, *Croat 73040* (MO, QCNE).

Cultivated plants. Ecuador. Cult. by Dewey Fisk, Florida, U.S.A., *G. Zhu 1508* (MO); cult. Marie Selby Botanical Gardens (75-461, vouchered by *Dodson 5951*), *Christenson 1576* (SEL), *Madison 4140* (SEL); Marie Selby Botanical Gardens (78-2173), *Dodson 7288* (SEL), *Christenson 1154* (SEL), *Croat 71798* (MO), *Plowman 10926* (F), *G. Zhu 1453* (MO); cult. MBG (vouchered by *Croat 72368*), *G. Zhu 1459, 1518* (MO); received from the Marie Selby Botanical Gardens (78-2173, vouchered by *Dodson 7288*), *G. Zhu 1453, 1495* (MO).

7. **Dracontium dubium** Kunth, Ind. Sem. Hort. Berol. 1844: 283. 1844. *Echidnium dubium* (Kunth) Engl., Pflanzenr. 4, fam. 23C: 38. 1911. TYPE: Pl. 88 in Schott, Gen. Aroid.,

1858: 88 (neotype, designated by Zhu, Boos & Croat (1998: 102)); Venezuela. Carabobo: Caño Paso Ancho, ca. 6 km S of Valencia, near El Paito, *G. S. Bunting 3677B* (epitype, designated by Zhu, Boos & Croat (1998: 102), MY!; isotypes, MO!, NY!). Figure 10.

Dracontium changuango G. S. Bunting, Phytologia 60: 302. 1986. TYPE: Venezuela. Carabobo: Caño Paso Ancho, ca. 6 km S of Valencia, near El Paito, 22 Jan. 1968, *G. S. Bunting & Trujillo 2856* (holotype, MY!; isotypes, MO!, NY!).

Tuber hemispherical, 5–17 cm diam., 6–9 cm thick, flat above, rounded and whitish to brown below, 3–36 cm below ground level; tubercles few, rounded or cylindrically elongated, 0.5–0.9 cm diam., 0.5–1.5 cm long, borne around the periphery of the tuber; roots whitish, 1–2 mm diam.; *cataphylls* 2 or 3, 3–36 × 1.5–8 cm, pink to light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–2.4 m long above ground, 2–4 cm diam. at midpoint, dark green or tinged brown, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth or sometimes with spiny projections; juvenile blade sagittate, or sagittately lobed; mature *blades* spreading horizontally, 1–1.2 m diam., subcoriaceous papyraceous, rarely fenestrate, never variegated, sometimes with abundant dark markings, semiglossy and dark green above, matte and medium green below; *middle division* twice trichotomously branched, 50–72 × 45–75 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 50–70 × 47–73 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent or free, each usually consisting of a single segment or a few segments or rarely each consisting of many segments; leaf segments bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, orbicular-ovate, at least some of the basal segments free, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or acute; *ultimate segments* 9–20 cm long, free from penultimate segments; other segments 10–20 cm long; penultimate segments confluent with the subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green or distinct from petiole, pale green, tinged brown, with irregular protuberances; tertiary veins obscure above and conspicuous below; *bracteoles* 1 or 2, 5–15(37) × 1.5–2 cm, white to pink (at apex), the longest one longer than the peduncle, covering up to ⅓ of the spathe. *Inflorescence* solitary or sometimes two, appearing before new leaf; *peduncle* 3–36 cm long above ground, 0.5–1 cm diam. at midpoint, often almost completely subterranean (to a few cm above ground level), mottled similar to petiole but lighter in color, white tinged pink, smooth; *spathe* 4–15 cm long, 2–5 cm wide, non-cymbiform, broadened at a certain point and differentiated into a proximal tube and a distal lamina (blade), non-cucullate or cucullate (slightly), arching to 45°, apex acuminate; 1–4 × 1.8–3.5 cm at widest point; lamina 2 or 3 times longer than the tube; inner surface covered with dense, translucent scales 1–2 mm long, olive-brown or red-purple, with translucent area obscure; outer surface maroon, matte; margins entire, broadly overlapping in the lower third; veins obscure inside and outside, similar to the spathe in color; *spadix* exposed (often extending above the spathe tube), stipitate, cylindric, brownish purple, 1.2–4.2 × 0.5–1.3 cm at anthesis, often with several appendages at apex, 0.2–0.5 cm long when present; stipe 0.2–0.8 × 0.4–0.5 cm at anthesis. Flower tepals 6 or 7, 1–2 mm long, 0.5–1 mm wide, brown-purple; stamens 6 or 7; filaments 0.5–1.5 mm long; anthers 0.8–1 mm long, slightly exserted; ovary bilocular or 3- to 5-locular, pale green; stigma 3-lobed, or 4-lobed; style 0.2–0.5 mm long above tepals, greenish, not persistent. *Infructescence* with spadix 4–6.5(10) × 2.6–3.5 cm in fruit, *berries* (1)3- or 4(5)-seeded, 1–1.5 cm diam., 1.2–1.7 cm thick, subglobose, 3- to 6-angular, apically truncate; young berries dark green; mature berries orange (or yellow), with or without some reddish dots or raphide cells, *seeds* 0.8–1 cm long, 0.5–0.7 cm diam., elongated or rounded, red-brown, laterally flattened; dorsal ridges obvious, more than 3, strongly to slightly interrupted, monomorphic, less than 0.5 mm thick, 0.8–1 mm high, smooth on both sides. Chromosome number $2n = 26$ (*Aristeguieta 12734*; Petersen, 1989).

Phenology. Flowering from late January to April; mature fruits from May to July.

Distribution and habitat. Dracontium dubium ranges from the Amazon basin to the Atlantic coast in Venezuela and is expected to be found in adjacent areas in Colombia and Guyana. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at elevations of 80 to 500 m.

Local names. "Changuango" (*Bunting 4432*, MY); "cuma pan" (*Liesner & González 5773*, MO).

Discussion. Dracontium dubium is character-

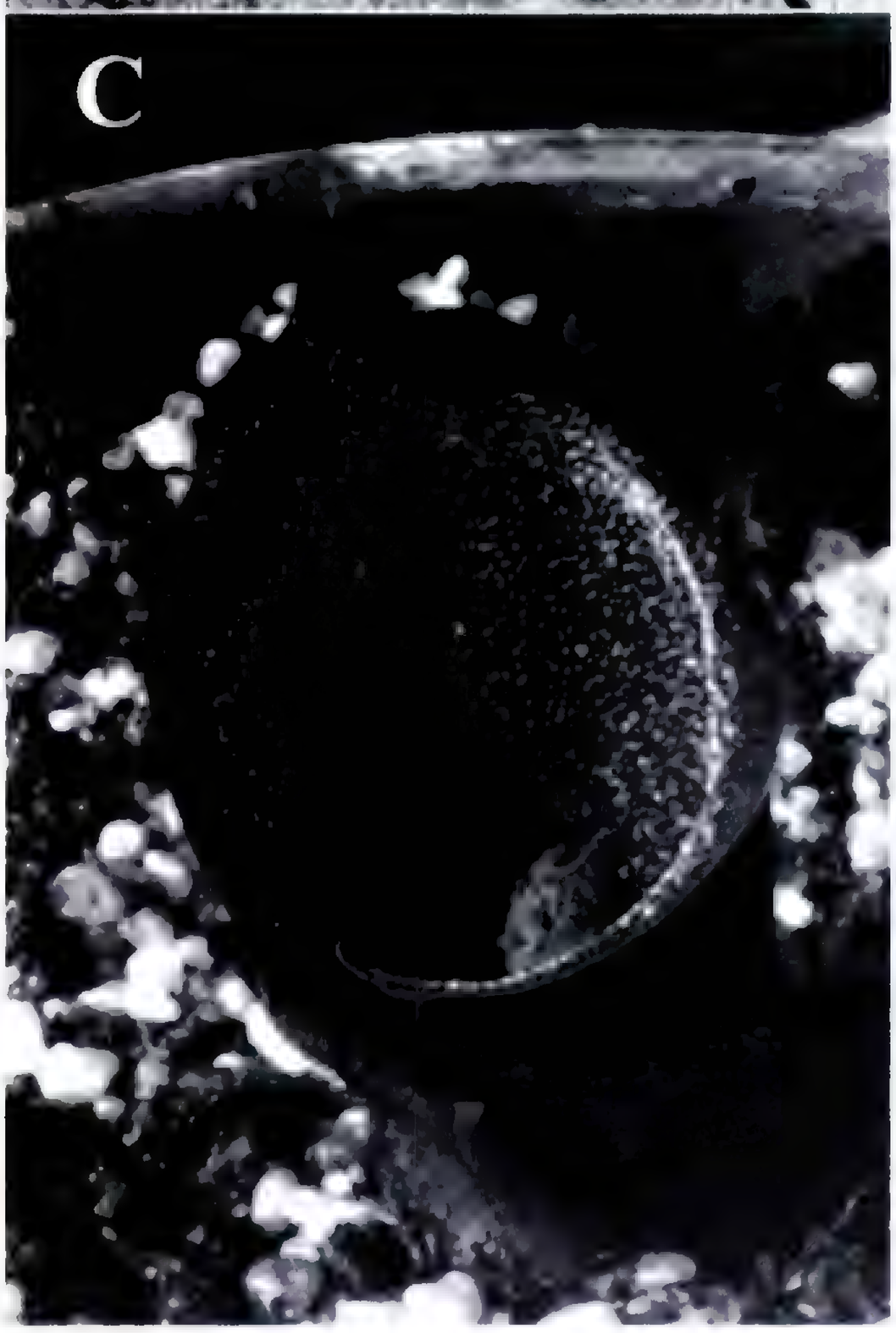

Figure 10. A–D, *Dracontium dubium*. —A. Leaf of cultivated plant at Munich Botanical Garden (*Aristeguieta 12734*). —B. Seeds in various positions (*Huber 1826*). —C. Inflorescence at anthesis (*Aristeguieta 12734*). —D. Type specimen of *D. changuango* G. S. Bunting (*Bunting & Trujillo 2856*).

ized by having the inner surface of the spathe covered with dense, translucent scales (1–2 mm long) and a spadix that often has apical appendages. *Dracontium purdieanum* is very similar in terms of its leaf, the relatively short inflorescences, the noncucullate spathe, and the occasional presence of appendages on the end of the spadix; it differs in having usually shorter peduncles (less than 5 cm above the soil) and in having seeds with three continuous ridges to 0.5 mm high.

Dracontium dubium Kunth was first collected by Richard Schomburgk during an expedition to British Guiana (Guyana) in 1840–1844 at the base of Mt. Curassawaka of the Kanuku Mountains, south of Nappi, and several living tubers were sent to the Botanical Garden of Berlin in 1843 (Roth, 1922: 387–388; 1923: 103). One plant bloomed in the Garden and was described by Kunth in the following year (Kunth, 1844). Schott (1860: 481) noted that there were fertile collections of this species at the Berlin Herbarium (B). However, no specimen of *D. dubium* was seen by Engler (in 1911: 39), who only cited "Bluehte im Bot. Garten zu Berlin Sept. 1844" (flowered in Berlin Botanical Garden in September 1844) under the species. Schott (1860) might very likely have only seen live specimens of the species since at Kunth's time, garden plants were often described and illustrated without preparing herbarium specimens (Paul Hiepko, pers. comm.). Kunth had apparently made a drawing of the inflorescences and some floral details of the species, which was deposited in the Berlin herbarium (Engler, 1911: 38, fig. 14A–F). More than a decade after the discovery of *D. dubium*, Schott (1857b), based on unspecified ovary and stigma details of the species, described the new genus *Echidnium*, giving the single species a new name, *E. schomburgkii*. In the following year, Schott (1858b: pl. 88) published a plate that included the inflorescence and floral details of this species under the name *E. schomburgkii*, which copied Kunth's drawing adding an inflorescence at anthesis and other floral details. Later, when he published the first comprehensive classification of the Araceae, Schott (1860) accepted the name *E. schomburgkii*, citing *D. dubium* as a synonym. Under contemporary rules of the ICBN (Greuter et al., 2000), *E. schomburgkii* is a superfluous name, since Schott should have used the name *E. dubium* for the transfer. Engler (1911) rectified this situation by publishing the combination *E. dubium* (Kunth) Engl.

Echidnium is ostensibly distinguished from *Dracontium* by having a unilocular ovary with two ovules (Schott, 1857b), as opposed to a bi- or plurilocular ovary in *Dracontium*. However, these characters have been shown to be either spurious (Zhu, 1995) or not to be good generic characters in this group (Bogner, 1985; Hay, 1988; Zhu, 1996). The two plates originated from the typical material of *D. dubium* (*Genera aroidearum*, pl. 88, Schott, 1858b; *Das Pflanzenreich*, 4 (23C): p. 38, fig. 14A–F, Engler, 1911) clearly demonstrated a plant of at least two locules. Schott's statement of a unilocular ovary was evidently erroneous based on his own illustration. Zhu (1995, 1996) noted that unilocular ovaries do not occur in *Dracontium* and this genus never has more than one ovule in each locule; these stand as generic traits of the genus. Therefore, *Echidnium* was accepted as a synonym of *Dracontium*, and *D. dubium* is the accepted name for the treated species (Zhu et al., 1998).

Additional specimens examined. VENEZUELA. **Amazonas:** alrededores de San Juan de Manapiare, *Girardi 16* (VEN); Atabapo, Canaripo, lower Río Ventuari, 20 km E of confluence w Río Orinoco, *Huber 1826* (MO); Santa Bárbara del Orinoco, near confluence of Río Orinoco and Río Ventuari, *Steyermark et al. 117171* (MO, VEN); Atures, Isla Castillito-San Fernando de Atabapo on Río Orinoco, outskirts of Siquita, *Bunting 3677A* (MY, NY); Caño Wedidi, upper Río Ventuari, *Lister 461* (K). **Apure:** Río Orinoco to Piedra La Villa, opposite Raudal Marimare, *Wurdack & Monochino 41392* (NY). **Barinas:** Res. For. Caparo, 26 km E of El Cantón, *Meier 435* (VEN). **Bolívar:** 1 km N of Paragua, *Liesner & González 5773* (MO, VEN); 1 km S of Quebrada La Flore, tributary Río Parguaza, *Steyermark et al. 131647* (MO). **Carabobo:** Caño Paso Ancho, 5–6 km S of Valencia on rd. to El Paito, *Bunting & Trujillo 2856* (MO, MY, NY). **Cojedes:** Quebrada Chumeo, Fundo La Leona, *Delascio 6818* (VEN). **Guárico:** Río Orituco, S of Calabozo, *Castillo 260* (VEN); Calabozo, *Aristeguieta 5381* (VEN). **Portuguesa:** Guanare, Fundo "El Chaparral," 16 km NW of Guanaré, *Aymard & Stergios 3807* (MO, PORT, VEN); Río María, NE of Boca de Monte, 28–32 km NNE of Guanaré, *Steyermark et al. 127097* (MO, PORT, VEN); Río Tucupido, *Rodriguez 158* (MY); Turen, Esta. de Silvicultura, *Ortega & Aristeguieta 1554* (MO, PORT); Pozo Blanco, Est. Biol., *Ortega 748* (MO, PORT).

Cultivated plants. Venezuela. Portuguesa, Turén (Villa Bruzual), cult. Munich Botanical Garden, Germany, *Aristeguieta 12734* (M); Amazonas, Atures, Aragua, Maracay, along the Río Orinoco, collected by G. S. Bunting, *Bunting 3677A*, *Bunting 3677B* (NY).

8. Dracontium gigas (Seem.) Engl., Monogr. Phan. 2: 284. 1879. *Godwinia gigas* Seem., J. Bot. 7: 313. t. 96, 97. 1869. TYPE: Fig. 1 in J. Bot. 7: t. 96 & 97, 1869 (lectotype, designated by Zhu (1994a: 407)); Nicaragua. Chontales: betw. Javalí Gold Mine & Quebrada de Las Lajas, 19 Mar. 1884, *Brown s.n.* (epitype, designated by Zhu (1994b: 407), K!). [Cult. at K, originally collected by B. Seemann.] Figures 2C, 11, 14D.

Tuber hemispherical, up to 20 cm diam., 12 cm

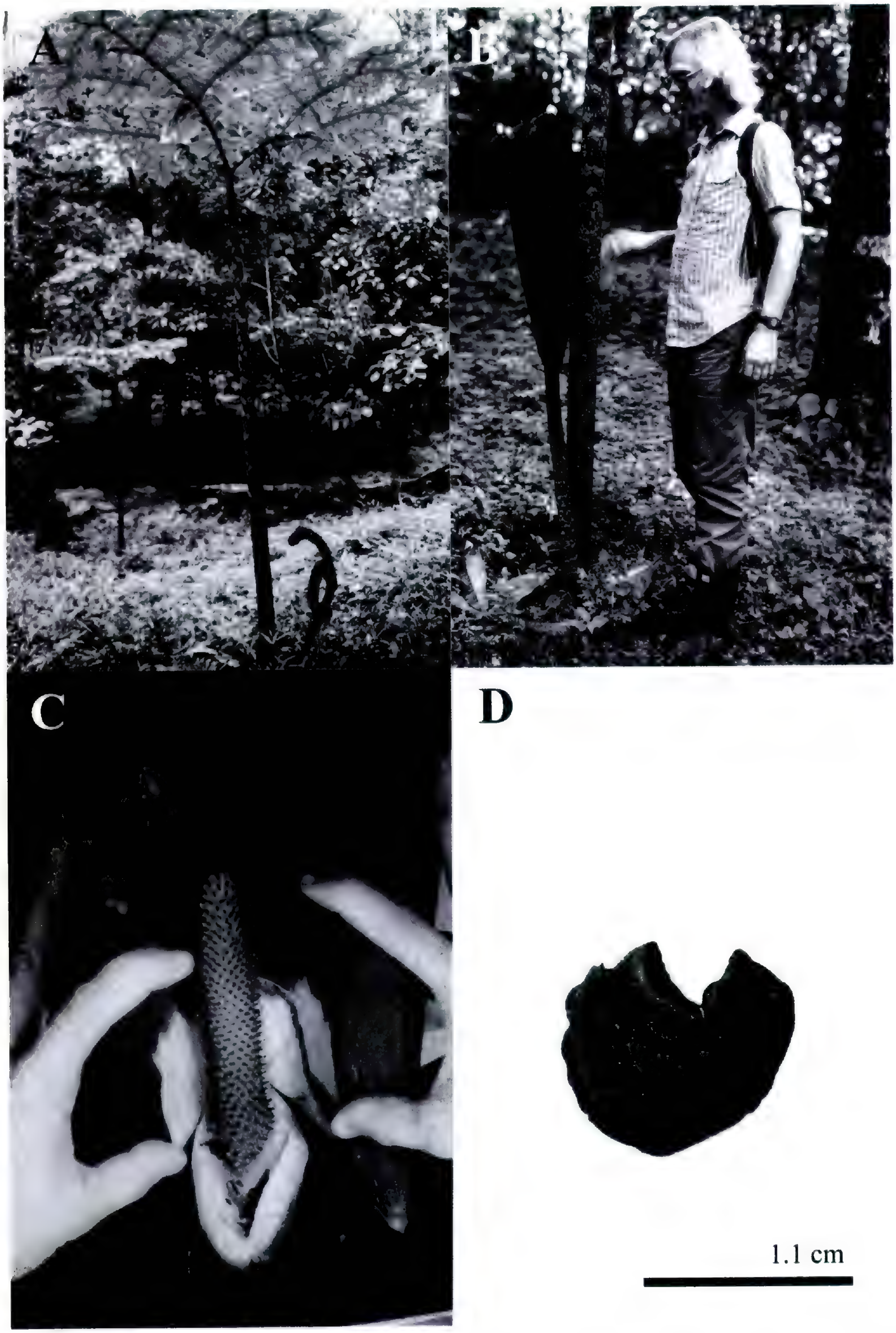

Figure 11. A–D, *Dracontium gigas*. —A. Plant in natural habitat at La Selva in Costa Rica (photo by G. G. Dimijian). —B. Flowering plant at anthesis with M. H. Grayum at La Selva (*Grayum 7911*). —C. Inflorescence at anthesis showing interior of spathe with spadix at anthesis. —D. Seed showing side view (*Beach 1490*).

thick, flat above, rounded and white to brown below, 5–60 cm below ground level; tubercles few, cylindrically elongated, 0.5–1 × 1–2 cm, borne around the periphery of tuber; roots 0.4 cm diam., white; *cataphylls* 4 to 7, up to 40 cm long (to 5 cm long above ground level), 4–10 cm wide, pink to light brown (when dry). *Leaves* solitary or sometimes two or more per tuber; *petioles* up to 3.4 m long above ground, up to 9.5 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blades* spreading horizontally, 1.5–2.5 m diam., subcoriaceous, rarely fenestrate, never variegated, without raphide cells or dark markings, glossy and medium green above, semiglossy and medium green below; *middle division* 3 times or more trichotomously branched, 1.4 × 1.8 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, 1.3 × 1.6 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent, each consisting of many segments; leaf segments often bilobed or rarely trilobed, oblanceolate or triangular, mostly confluent with each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices often caudate, or sometimes acute; *ultimate segments* 10–16(–20) cm long, confluent with penultimate segments; other segments 10–20 cm long; penultimate segments confluent with the subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, confluent with each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins conspicuous above and obscure below; *bracteoles* 3 or 4, 10–60 × (sometimes 5–10 cm above ground level) 4–6 cm, light brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. *Inflorescence* solitary, appearing before new leaf; *peduncle* 30–120 cm long above ground, 3.5–6 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, dark green or brownish green, with irregular protuberances in lower half; *spathe* 58–78 × 13–15(–21) cm, cymbiform, cucullate, erect or slightly arching, apex obtuse; inner surface semiglossy, red-purple or purple-red, with a translucent area obvious, 4–6.5 cm high, shorter than spadix; outer surface maroon tinged brown, matte; margins entire, broadly overlapping in the lower two-thirds; veins purple, obscure inside and outside (slightly impressed inside), conspicuously darker or paler than the spathe on top; *spadix* hidden, sessile or stipitate, cylindric, brown-purple, 9–16 × 1.5–1.8 cm at anthesis, never with appendages at apex. Flower tepals 6 to 8(9), 3.5–5 mm long, 1.5–2 mm wide, light brown tinged green; stamens 8 to 17(19); filaments 1–3.5 mm long; anthers 1–1.5 mm long, completely exserted; ovary 3- to 4-locular, pale green; stigma 3-lobed; style 4–6 mm long above tepals, dark purple, persistent. *Infructescence* with spadix 20–30 cm long, 4–6 cm diam. in fruit; *berries* often 2-seeded, 1.8 × 1.5 cm, 4- to 5-angular or globose (rarely), apically truncate; young berry unknown; mature berry orange or purple-brown, with or without some reddish dots or raphide cells; *seeds* 1–1.2 cm diam., rounded, reddish brown, laterally raised; dorsal ridges obvious, 3, continuous, less than 0.5 mm thick. Chromosome number $2n = 26$ (*Bogner 1267*; Petersen, 1989).

Phenology. Flowering from December to April; mature fruits from April to August.

Distribution and habitat. *Dracontium gigas* ranges from central Nicaragua (Chontales), along the Atlantic slope to central Costa Rica (Heredia, Limón). It occurs in *Tropical moist forest* (T-mf) and *Premontane wet forest* (P-wf) life zones (Holdridge et al., 1971), at elevations of 15 to 100(–450) m.

Discussion. *Dracontium gigas* has the largest spathes in the genus, ranging from 58 to 78 cm long and 13 to 15(–21) cm wide. It is the most well-known species horticulturally, especially in Europe. It regularly blooms in European gardens and private nurseries, but has never been reported flowering in gardens of the New World. This species propagates rapidly by means of tubercles. It is also a fast grower, capable of growing a couple of inches in height overnight. It is often a big attraction when it blooms.

Dracontium gigas is easily confused with *D. pittieri* in sterile condition. The mature leaves of these species are almost identical. However, leaves of *D. pittieri* tend to have more raphide cells, especially when young, and less leaf tissue along the rachis and at the branching points. The upper half of the petiole is often smooth and unicolored in *D. pittieri*, while often mottled and with projections in *D. gigas*. Despite strong vegetative similarities, these two species are distinct in their inflorescence morphology. *Dracontium gigas* has a large spathe and a short peduncle, which is always less than twice as long as the spathe. *Dracontium pittieri* has a much longer peduncle, 5 to 8 times longer than the spathe. The spathe of *D. gigas* is more or less hood-

ed at the apex, with the margins broadly overlapping and completely covering the spadix. The spathe of *D. pittieri* is open at the apex with the margins scarcely overlapping, such that the spadix is exposed. The translucent area at the base of the inner spathe surface extends much higher than the spadix in *D. pittieri*, while it never exceeds the height of the spadix in *D. gigas* (Zhu, 1994a).

Since there is no type designated in the protologue of *Godwinia gigas* Seem., the basionym of *Dracontium gigas* (Seem.) Engl., a plate from the original material, fig. 1 in J. Bot. 7: t. 96 & 97, 1869, was designated as the lectotype of *Godwinia gigas* (Zhu, 1994a). Since this lectotype does not contain enough information to identify *D. gigas* from *D. pittieri*, a fertile specimen prepared by N. E. Brown (*Brown s.n.*, K) was designated as an epitype for *D. gigas* to ensure the accurate application of these names (Zhu, 1994a).

Additional specimens examined. COSTA RICA. *Valerio 678* (MO). **Alajuela:** Canas-Upala, Río Zapote, 1.8–5 km S of Río Canalete, *Burger & Baker 9999* (F, MO, US); San Carlos, *Roig 11* (CR, F). **Heredia:** Braulio Carrillo, Rara Avis, trail El Atajo and Catarata, *G. Zhu 1154* (MO); La Selva, *Beach 1490* (DUKE, MO); Río Sarapiquí at Chilamate, *Croat 68381* (B, M, MO); Sarapiquí, near Puerto Viejo, *Valerio 24* (USJ), 15 Aug. 1993, *G. Zhu 1519* (MO). **Limón:** 10 km NW of Guápiles, *Gómez 18513* (MO); Río Reventazón below Cairo, *Standley & Valerio 48885* (US); Hacienda Tapezco-Hda., La Suerte, 29 air km W of Tortuguero, *Davidson 8624* (MO, RSA); Siquirres, *Dodge 5622* (F); Bataau, *Lehmann 246619* (CR). NICARAGUA. **Chontales:** received from Mr. Fitch in spirits (on sheet #6 of *Brown s.n.*, 30 Dec. 1878), *Bull s.n.* (K). **Río San Juan:** Caño Chontaleño, 20 km NE of El Castillo, *Neill & Vincelli 3512* (MO); Res. Indio-Maiz, San Juan del Norte, Río Indio, *Rueda et al. 8615* (MO); El Castillo, Sábalos, comarca Las Maravillas, *Rueda et al. 2869* (MO), *5225* (MO). **Zelaya:** Cerro Saslaya-San José Hormiguero, Caño Sucio-Loma Mollejones, *Stevens 7007* (M, MO); Stawas, 1 km N of Río Grande de Matagalpa, 8 km N of La Cruz, *Neill 4336* (MO); drainage of Ríos Punta Gorda, Alemán and Zapote, *Shank & Molina 4953* (GH, US); E of comarca del Salto del León, *Rueda et al. 3390* (MO); Mun. Nueva Guina, Res. Indio-Maiz, *Rueda et al. 10190* (MO); este del poblado de Nueva Atlanta, *Rueda et al. 3295* (MO).

Cultivated plants. Nicaragua. Cult. at Berlin Botanical Garden, Germany, *Anonymous s.n.* (M); Chontales, originally collected by Seemann, W. Bull's establishment, between the Javalí Gold Mine and the Quebrada de Los Lajas, cult. Royal Botanical Gardens at Kew, Great Britain, *Brown s.n.* (GH, K), *Brown s.n.* (GH), *Brown s.n.* (K). Costa Rica. Limón, originally collected by M. Birdsey, cult. at Robert and Catherine Wilson Botanical Garden at Las Cruces, *G. Zhu 1156* (MO); originally collected by Clarence Horich, Alajuela, between San Carlos & San Pedro Cutris, cult. at Munich Botanical Garden, *Bogner 1267* (M); originally collected by John Banta, Llanuras de San Carlos, betw. Vasconia and San Pedro Cutris, cult. MBG, *Croat 71840* (MO), vouchered by *G. Zhu 1156, 1517* (MO); vouchered by *G. Zhu 1159, 1467* (MO); vouchered by *Croat 68381, G. Zhu 1481* (B, M, MO).

9. Dracontium grandispathum G. Zhu & Croat, sp. nov. TYPE: Ecuador. Napo: Cañon de los Monos, 15 km N of Coca near Río Coca, Hacienda of Hector Noboa, 0°20′S, 77°01′W, 250 m, 9 Apr. 1985, *W. Palacios, D. Neill, M. Baker & J. Zaruma 311* (holotype, MO!). Figure 12.

Petiolus 1.25–2.75 m longus; lamina 55–75 cm longa, 55–60 cm lata; pedunculus 1–1.35 m longus, 1.5–2 cm diam.; spatha 45–50 cm longa, 10–15 cm lata, cucullata basi; extus impolita, olivacea; intus velutina, purpurea; spadix 3–5.5 cm longus, 0.5–1 cm diam.; tepala 5–6; semina rubra, 0.6–0.7 diam.

Tuber hemispherical, 10–18 cm diam., 6–10 cm thick, flat above, rounded and white to brown below, 12–20 cm below ground level; *cataphylls* 3 to 4, 12–21 × 2–3 cm, light brown, reaching or surpassing ground level. Leaves solitary; *petioles* 1.25–2.75 m long above ground, 2–3.5 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blade* spreading horizontally, 1–1.2 m diam., subcoriaceous, sometimes fenestrate, never variegated, without raphide cells or dark markings, glossy and medium green above, semiglossy and medium green below; *middle division* twice trichotomously branched, 55–75 × 50–60 cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 55–75 × 55–60 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections often confluent, each consisting of many segments; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate or lanceolate, mostly free from each other in each division, often without contrastingly smaller rounded or triangular segments; apices acuminate; *ultimate segments* 25–30 cm long, often free from penultimate segments; other segments 15–20 cm long; penultimate segments free from subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins conspicuous above and weakly raised below; *bracteoles* 3 or 4, 12–22 × 2–3 cm, light brown, the longest one much shorter than the peduncle, confined to

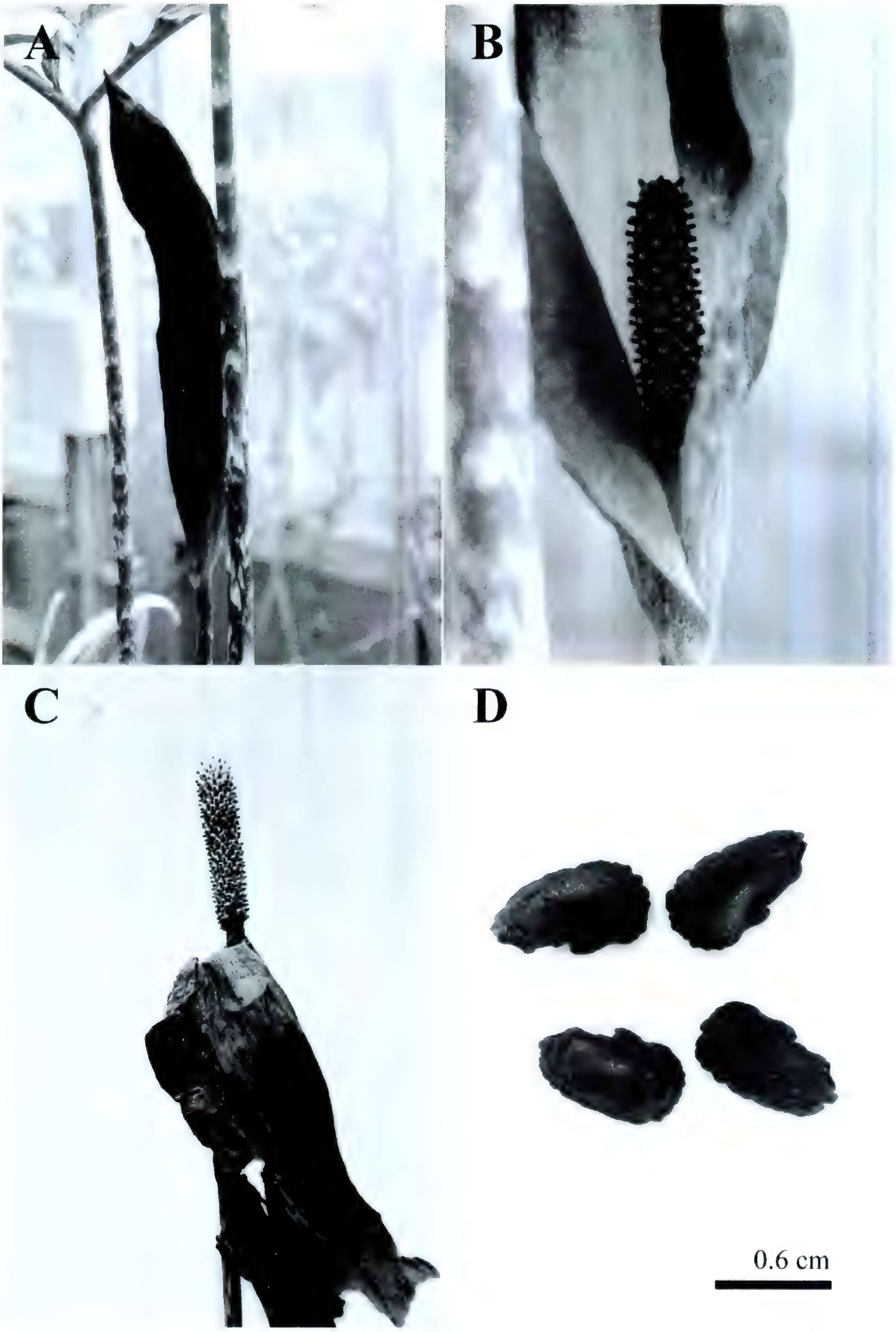

Figure 12. A–D. *Dracontium grandispathum*. A, B. (*Croat 75207*). —A. Inflorescence, side view. —B. Close-up of inflorescence showing front view of spathe with spadix. —C. (*Pinkley 60-B*). Immature infructescence. Photo by H. Pinkley. —D. (*Cerón & Cerón 3070*). Seeds in side view.

the base. *Inflorescence* solitary, appearing before or after new leaf; *peduncle* 100–135 cm long above ground, 1.5–2 cm diam. at midpoint, more than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, smooth or spiny projections; *spathe* 45–50 × 10–15 cm, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucullate or non-cucullate, erect or slightly arching, apex acuminate (very broadly); 10–15 × 10–15 cm at widest point; lamina 2 to 3 times longer than the tube; inner surface semiglossy, maroon or purple-red or olive-brown, with translucent area moderately conspicuous, 12–15 cm high, 1.5 to 3 times longer than spadix; outer surface olive-brown or green or green tinged brown, matte; margins entire, broadly overlapping at the base; veins conspicuous inside and raised outside, conspicuously darker or paler than the spathe, purple; *spadix* hidden, stipitate, cylindric, pale green or light brown, 3–5.5 × 1–1.5 cm at anthesis, never with appendages at apex; stipe 0.5–1 × 0.5–0.7 cm at anthesis, light brown or dark purple. Flower tepals 5 to 6, 1–3 mm long, 1–2 mm wide, light brown or purple; stamens 7 to 11; filaments 1–2 mm long; anthers 0.5 mm long, hidden or slightly exserted; ovary 3-locular, pale green; stigma unlobed, or 3-lobed; style 0.5–1 mm long above tepals, dark purple, persistent. *Infructescence* with spadix 12–18 × 2.5–3.5 cm in fruit; *berries* 1- or 2-seeded, 0.5–0.6 cm diam., 0.8–1 cm thick, obliquely obovoid, apically rounded; young berry light green; mature berry orange, without reddish dots and raphide cells; *seeds* 0.6–0.7 cm diam., rounded, red-brown, laterally flattened; dorsal ridges obvious, 3, often strongly interrupted, with the central ridge contrastingly raised, more than 1 mm thick, 0.1–0.2 mm high, warty along ridges.

Phenology. Flowering from November to May; mature fruits from March to December.

Distribution and habitat. *Dracontium grandispathum* is known only from Amazonian Ecuador (Morona-Santiago, Napo, and Pastaza). It occurs in *Premontane moist forest* (P-mf) and *Tropical montane moist forest* (TM-mf) life zones (Holdridge et al., 1971) at 250 to 1200 m.

Local names. "Nantaymo" (*Aulestia 1823*, MO); "pitalala para" (*Jipa et al. 968*, F).

Discussion. *Dracontium grandispathum* is vegetatively similar to the sympatric *D. spruceanum*, but differs in having a much a larger (hence, the name *grandispathum*) and usually hooded spathe 45–50 × 10–15 cm versus 20–35 × 3–6 cm in *D. spruceanum*. The spathe of *D. grandispathum* is often abruptly acuminate apically and that of *D. spruceanum* is gradually acuminate apically.

Paratypes. ECUADOR. **Morona-Santiago:** Méndez-Morona, km 45–63, *Dodson et al. 17756* (MO). **Napo:** Baeza-Tena, 5 km N of Jondachi, *Harling & Andersson 16404* (GB); Narupa-Coca, 18 km E of Narupa, *Hammel & Wilder 17283* (MO); Cantón Lago Agrio, Parroquia Dureño, Cofán-Dureno, *Cerón & Cerón 3070* (MO, QCA); Dureño, *Pinkley 60* (ECON); Cantón Tena, Jatún Sacha, *Palacios 4242* (MO); Par. Nac. Yasuní, Carretera Maxus, km 1, Pompeya, *Aulestia 1823* (MO, QCNE); Yasuní, Añangu, *Luteyn et al. 9021* (MO, QCA); Río Tiputini, NW of confluence of Río Tivacuno, *Romoleroux 2110* (QCA), *2135* (QCA), *2360* (QCA), *2649* (QCA); San José de Payamino, 40 km W of Coca, *Jipa et al. 968* (F). **Pastaza:** Montalvo, Río Bobonaza, *Løjtnant & Molau 13549* (AAU). **Pichincha:** Cantón-Santo Domingo de los Colorados, *Cerón et al. 29051* (QAP).

Cultivated plants. Ecuador. Napo, Tena, 27 May 1993, collected by Scott Hyndman, vouchered as *T. B. Croat 75207* (MO); *G. Zhu 7528* (MO); vouchered by *Pinkley 60, Pinkley 294* (ECON), cult. at MBG.

10. Dracontium grayumianum G. Zhu & Croat, sp. nov. TYPE: Panama. Darién: near Par. Nac. Darién, 4 km NE of Piji Vasal village, trail W of ANCON Agricultural Station, 8°04′N, 77°46′W, 100 m, 27 July 1994, *G. Zhu & T. B. Croat 1506* (holotype, MO!; isotypes, B!, F!, GH!, K!, M!, NY!, PMA!, SCZ!, SEL!, UC!, US!). Figures 1D, 2A, 13.

Petiolus 1–2.2 m longus; lamina 0.8–1 cm longa, 0.7–1 cm lata; pedunculus 1–10(–30) cm longus, 1–1.8 cm diam.; spatha (6)9–15 cm longa, 2.5–4 cm lata, cucullata basi; extus impolita, purpurea; intus velutina, purpurea; spadix 2–3.5 cm longus, 0.8–1.3 cm diam.; baccae 1–2 cm diam.; semina brunneola, 0.8–1 cm longus, 0.6–0.7 cm diam.

Tuber hemispherical, 10–18 cm diam., 6–10 cm thick, flat above, rounded and white to brown below, 10–20 cm below ground level; tubercles few, cylindrically elongated, 0.8–1.2 cm diam., 1–3 cm long, borne around the periphery of tuber; roots white to 0.4 cm diam.; *cataphylls* 3, 10–30 × 5–8 cm, white or pink and light brown, 5–15 cm long above ground. *Leaves* solitary; *petioles* 1–2.2 m long above ground, 2–6 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blade* spreading horizontally, 1–1.5 m diam., papyraceous, sometimes fenestrate, never variegated, sometimes with abundant raphide cells and dark markings, glossy and dark green above, semiglossy and medium green below; *middle division* 3 times or more trichotomously branched, 0.8–1 × 0.7–1 cm, with terminal

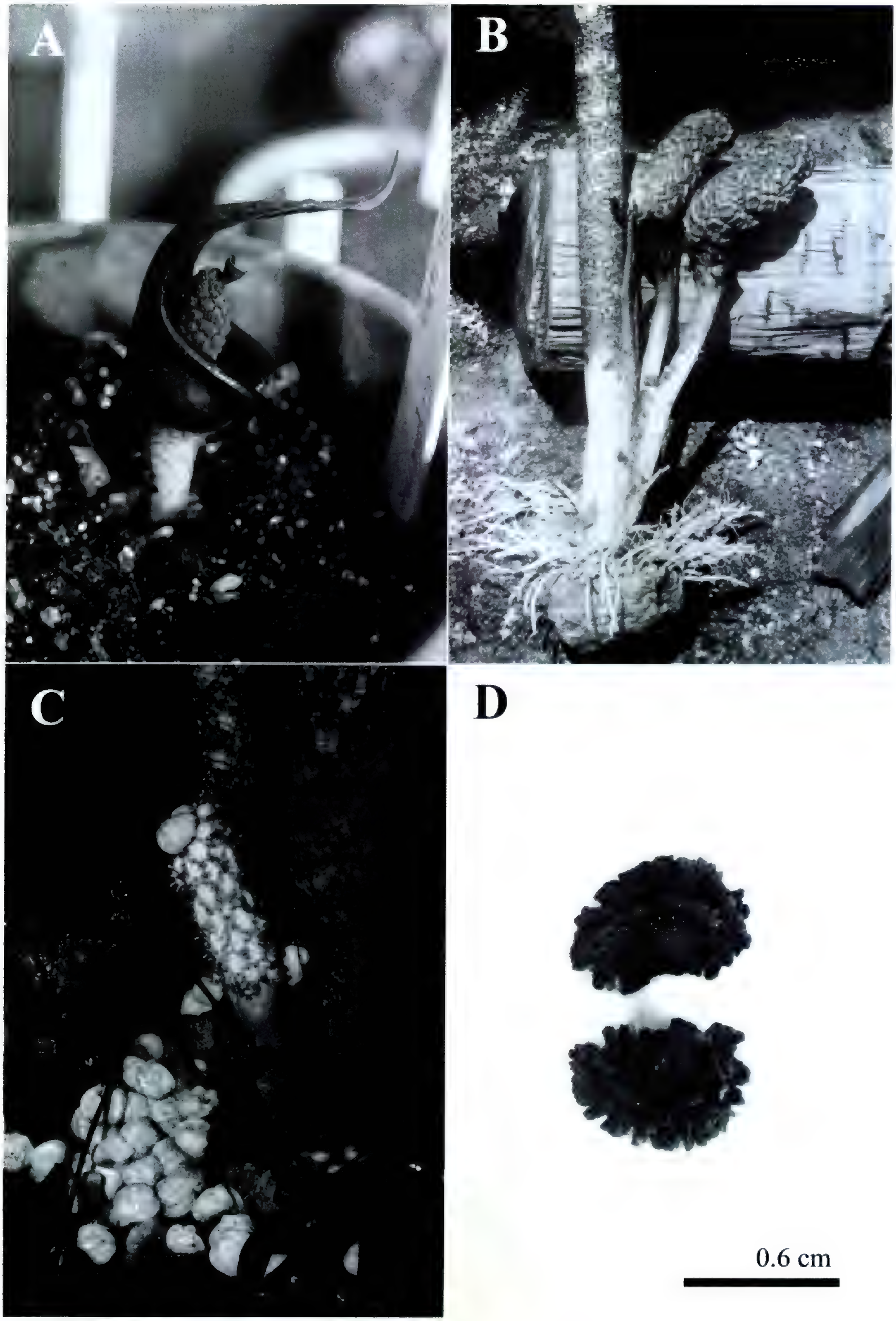

Figure 13. A–D, *Dracontium grayumianum*, type specimen (*G. Zhu & Croat 1506*). —A. Inflorescence at anthesis in side view. —B. Tuber, petiole base, and cluster of immature infructescences. —C. Spadix with mature berries, mostly already fallen. —D. Seeds in side view.

subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, 0.85–1 × 0.7–1.1 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; leaf segments bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, lanceolate, mostly free in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or acute, or caudate (rarely); *ultimate segments* 12–15 cm long, confluent with penultimate segments (often); other segments 6–16 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, with spiny projections; tertiary veins conspicuous above, or weakly raised below; *bracteoles* 5–15(–35) cm long, 2–3(–5) cm wide, light brown, the longest one longer than the peduncle, covering the basal half or more of the spathe (often). *Inflorescences* solitary or sometimes two, appearing before new leaf; *peduncle* 1–10(–30) cm long above ground, 1–1.8 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, whitish tinged pink or gray or whitish green, smooth; *spathe* (6–)9–15 × 2.5–4 cm, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucullate, arching 45°–90°, apex acuminate; 2.5–3 × 2–3 cm at widest point; lamina similar to the tube in length, or 3 to 5 times longer than the tube; inner surface semiglossy, maroon, with translucent area obscure; outer surface maroon or olive-brown, matte; margins entire, broadly overlapping at the base; veins obscure inside and raised outside (slightly), conspicuously darker or paler than the spathe, purple; *spadix* exposed, stipitate, cylindric, brown or purple, 2–3.5 × 0.8–1.3 cm at anthesis, sometimes with one to a few appendages at apex, 0.3–0.5 cm long when present; stipe 0.5–2 cm long, 0.5–1.5 cm diam. at anthesis, brown. Flower tepals 5 to 7, 1–4 mm long, 0.5–1 mm wide, light brown; stamens (5)6 to 8; filaments 3 mm long; anthers 1 mm long, slightly exserted; ovary bilocular, pale green; stigma 2-lobed; style 1–2 mm long above tepals, dark purple, persistent. *Infructescence* with spadix 8–15 cm long, 3.5–5.5 cm diam. in fruit; *berries* 4-seeded, 1–2 cm diam., 1–1.2 cm thick, narrowly clavate, apically truncate; young berry light green; mature berry orange, with or without some reddish dots or raphide cells; *seeds* 0.8–1 cm long, 0.6–0.7 cm wide, reniform, light brown, laterally flattened; dorsal ridges obvious, 5 to 6, strongly interrupted, monomorphic, less than 0.5 mm thick, 1.5–2 mm high, smooth on both sides.

Phenology. Flowering from March to April (June); mature fruits from March to August.

Distribution and habitat. Dracontium grayumianum ranges from southern Panama (Darién and San Blas) to the central Pacific coastal region in Colombia (Chocó and Valle). It occurs in the *Tropical wet forest* (T-wf) life zone (Holdridge et al., 1971) at elevations of 5 to 100 m.

Discussion. Dracontium grayumianum is closest in appearance to *D. soconuscum*, especially in leaf size, shape, and form as well as a similar inflorescence; however, *D. soconuscum* differs in having seeds with 3 very short (0.1–0.5 mm high), dorsal ridges instead of 5 to 6 strongly interrupted (1.5–2 mm high) dorsal ridges.

The species honors Michael H. Grayum of the Missouri Botanical Garden, an aroid specialist, and one whose familiarity with the many aspects of plant taxonomy helped immeasurably with the completion of this work on *Dracontium*.

Paratypes. COLOMBIA. **Chocó:** Río Bicordó, above Noanamá, *Forero et al. 4718* (COL); Río Cacarica, *Romero 6357* (COL); Río San Juan, near Palestina, *Forero et al. 3800* (COL); Zona de Urabá, Cerros do Cuchillo, Camino Cuchillo Negro a Cumbre Noroeste rd., *Cárdenas 1805* (JAUM). **Valle:** Chocó region, Río Calima, La Trojita, *Cuatrecasas 16474* (F); Finca La Cabaña, camino a la Patricia, *Rentería 4314* (JAUM); Finca La Cabaña, Camino al Río León, *Rentería 4220* (JAUM). PANAMA. **Darién:** Piji Vasal, *G. Zhu & Croat 1507* (MO); Pinogana, E of El Real, *Pittier 6546* (US); Río Chucunaque, Yaviza, Quebrada Barbua, *Stern 93* (GH, MO); km 16 to Yaviza along Q Uvital off Río Chucunaque, *Duke 5103* (GH, MO). **San Blas:** Río Cangandí, Pueblo Cangandí, *Herrera 252A* (MO).

11. **Dracontium guianense** G. Zhu & Croat, sp. nov. TYPE: French Guiana. Haut Oyapock, Ouest de Trois Sauts Crique Euleupousing, Saut Beco, 15 July 1975, *J. de Granville & Cremers 1129* (holotype, CAY!). Figure 14A, B, C.

Petiolus usque 2.5 m longus; lamina 40–50 cm longa, 35–40 cm lata; pedunculus 30–40 cm longus, 0.5 cm diam.; spatha 9–10 cm longa, 4–5 cm lata; extus impolita, purpurea; intus velutina, purpurea; spadix 2.8 cm longus, 0.6 cm diam.; baccae 0.7–1 cm diam.; semina fusca, 0.65 cm diam.

Tuber hemispherical, 10–15 cm below ground

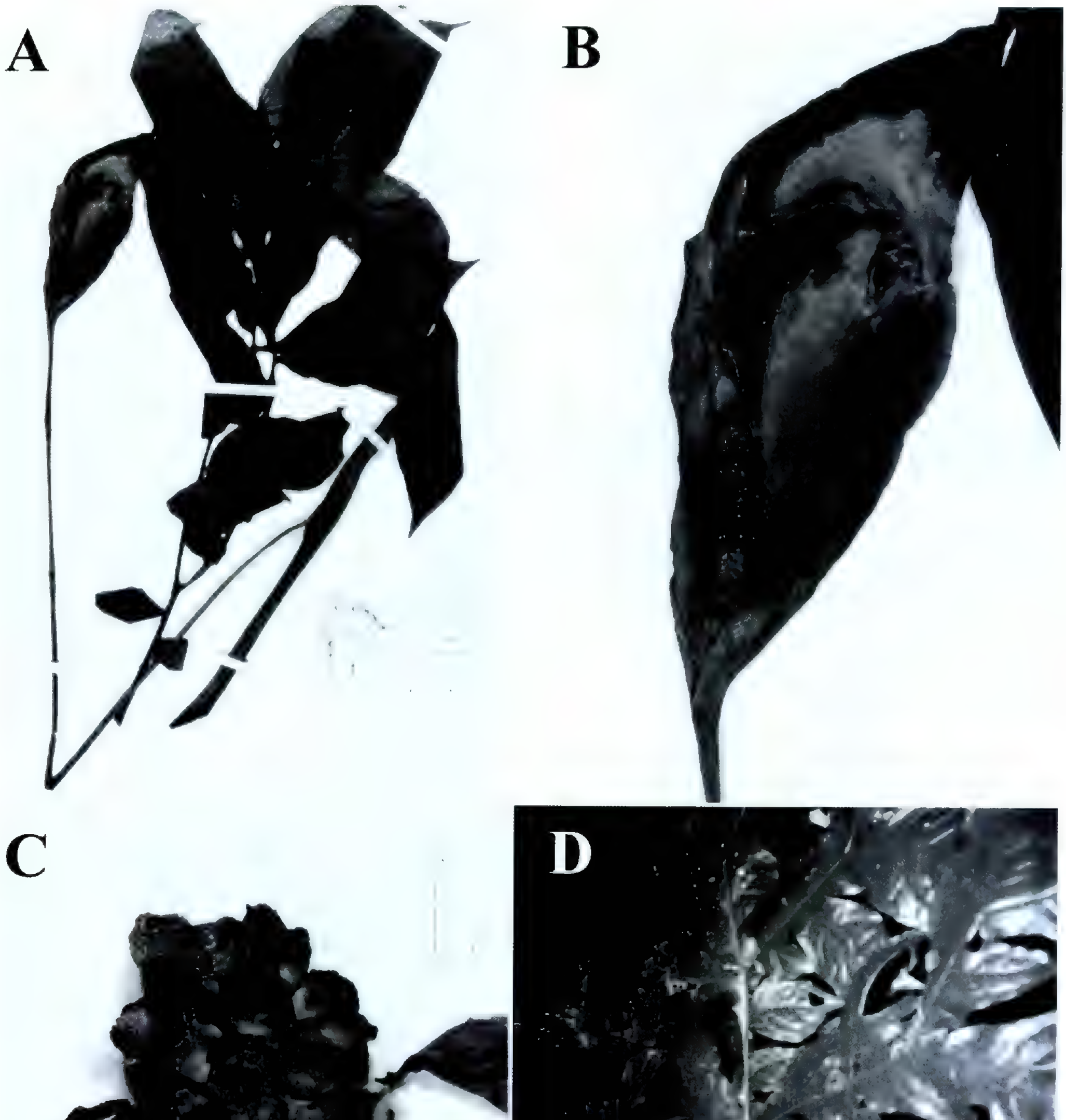

Figure 14. A–C, *Dracontium guianense*. —A. Holotype specimen, leaf and inflorescence (*de Granville & Cremers 1129*, CAY). —B. Close-up of inflorescence from *de Granville & Cremers 1129* (CAY). —C. Infructescence with mature fruits (*Grenand 1277*). —D. *D. gigas*. Leaf of plant at La Selva, Heredia Prov., Costa Rica.

level; *petioles* 2.5 m long above ground, 1.2 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth; mature *blades* 80–100 cm wide, subcoriaceous, rarely fenestrate, never variegated, without raphide cells or dark markings, glossy and dark green above, semiglossy and medium green below; *middle division* once or twice trichotomously branched, 40–50 × 35–40 cm, with terminal subdivision never divided into sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 40–45 × 35–40 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate; *ultimate segments* 15–17 cm long, free from penultimate segments; other segments 3–15 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and weakly raised below; *bracteoles* 1, 10–15 cm long, 0.5–1 cm wide, light brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. *Inflorescence* solitary, appearing after new leaf; *peduncle* 30–40 cm long above ground, 0.5 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, smooth; *spathe* 9–10 × 4–5 cm, cymbiform, non-cucullate, erect or slightly arching up to 45º angle, apex acuminate; inner surface semiglossy, maroon, with translucent area obscure; outer surface maroon tinged brown, matte; margins entire, hardly overlapping at the base; veins obscure or conspicuous inside, conspicuously darker or paler than the spathe; *spadix* sessile, cylindric, brown or brown-purple, 2.8 × 0.6 cm at anthesis, never with appendages at apex. Flower tepals 4 to 5, 2–3 mm long, 1–2 mm wide, light brown; stamens 4 to 6; filaments 2–3 mm long; anthers 0.5 mm long, completely exserted; ovary bilocular, pale green; stigma 2- or 3-lobed; style 0.5 mm long above tepals, green, persistent. *Infructescence* with spadix 4.3 cm long, 3.2 cm diam. in fruit; *berries* 2-seeded, 0.7–1 cm diam., 1 cm thick, subglobose, 3- to 6-angular, apically truncate; young berries medium green; mature berries orange, without reddish dots and raphide cells; *seeds* ca. 0.65 cm diam., rounded, dark brown, laterally convex; dorsal ridges obvious, 3, continuous, more than 1 mm thick, 0.1 mm high, finely decorated with small cells (pits) on both sides.

Phenology. Flowering known only in July; mature fruits are known only in May.

Distribution and habitat. *Dracontium guianense* is known only from the type locality in French Guiana near the border with Brazil (Pará); it will likely be found in Brazil. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971) at ca. 100 m.

Local names. "M y kala" (*de Granville & Cremers 1129*, CAY).

Discussion. *Dracontium guianense* is very similar to *D. polyphyllum*, but differs in having a much longer peduncle (more than 30 cm above ground level).

Paratypes. FRENCH GUIANA. Haut Oyapock, Ouest de Trois Sauts Crique Euleupousing, saut Beco, 10 May 1996, *Grenand 1277* (CAY); Piste de St. Elie, 6 Nov. 1982, *Riera 415* (CAY).

12. Dracontium longipes Engl., Bot. Jahrb. Syst. 37: 122. 1905. TYPE: Brazil. Acre: Belem at Juruá Miry, 8°S, 72°59′W, Sep. 1901, *E. Ule 5781* (holotype, B!; isotype, B!). Figure 15.

Tuber hemispherical, 10–15 cm diam., 6–10 cm thick, flat or slightly sunken above, rounded and whitish to brownish below, 10–25 cm below ground level; tubercles abundant, borne around the periphery of tuber; roots strong; *cataphylls* 1 to 3, 10–25 × 1–3 cm, light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–2 m long above ground, 3–4 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blades* spreading horizontally, 1–1.2 m diam., papyraceous, sometimes fenestrate, never variegated, sometimes with abundant raphide cells, semiglossy and dark green above, matte and medium green below; *middle division* 3 times or more trichotomously branched, 0.6–0.75 × 0.5–0.6 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, 0.45–0.7 × 0.5–0.6 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections

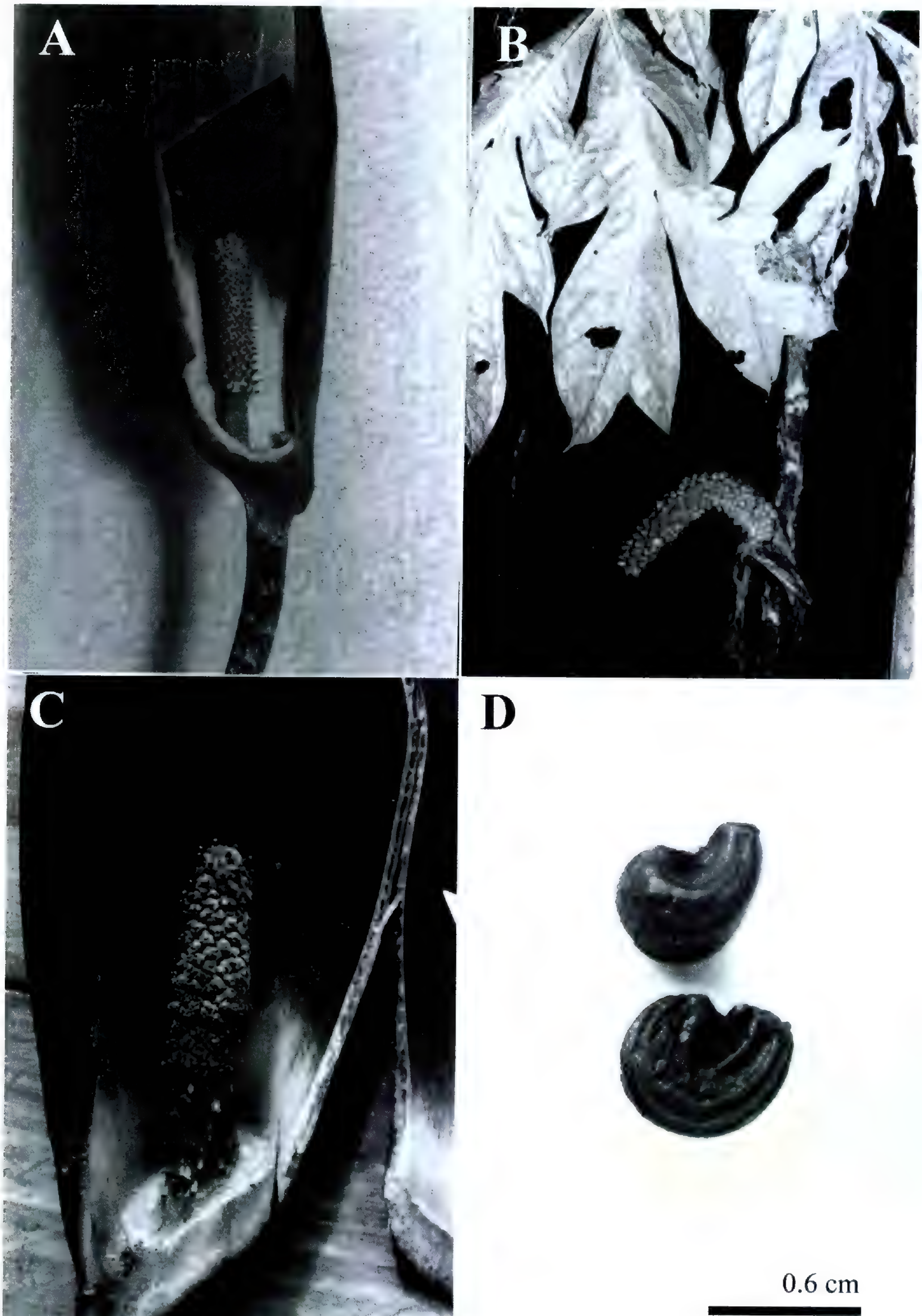

Figure 15. A–D, *Dracontium longipes*. —A. Inflorescence with the lower portion cut away to expose the spadix. —B. Live plant with portion of leaf and infructescence with persistent spathe. —C. Lower portion of spathe cut open showing close-up of spadix (*Croat 85460*). —D. Seeds in side view (*Croat 72368*).

free; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices caudate; *ultimate segments* 10–15 cm long, confluent with penultimate segments; other segments 9–16 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, sometimes with spiny projections; tertiary veins obscure above and weakly raised below; *bracteoles* 1 or 2, 10–25 × 1–2 cm, dark brown, the longest one much shorter than the peduncle, confined at the base. *Inflorescence* solitary, appearing before new leaf; *peduncle* 60–100 cm long above ground, 1–2 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, dark green, smooth or with irregular protuberances and spiny projections; *spathe* 23–25 cm long, 5–6 cm wide, cymbiform, cucullate, erect or slightly arching, apex acuminate; inner surface velvety, maroon, with translucent area obvious, 2–4 cm high, as long as spadix; outer surface violet-purple tinged green, matte; margins entire, broadly overlapping in the lower half; veins conspicuous inside, conspicuously darker or paler than the spathe, brownish; *spadix* hidden, stipitate, cylindric, light brown or purple, 2–3.5 × 0.5–0.7 cm at anthesis, never with appendages at apex; stipe 0.5–1 cm long, 0.4–0.5 cm diam. at anthesis. Flower tepals 4 to 6, 1–1.5 mm long, 0.5–1 mm wide, light brown; stamens 7 or 8; filaments 0.5 mm long; anthers 0.5 mm long, hidden; ovary bilocular, pale green; stigma 2- or 3-lobed; style 1–1.5 mm long above tepals, brownish purple, persistent. *Infructescence* with spadix 4–5 cm long, 2–2.5 cm diam. in fruit, *berries* 1-seeded, 0.4–0.6 cm diam., 0.5–0.8 cm thick, obliquely obovoid, apically rounded; young berries medium green; mature berries color unknown, without reddish dots and raphide cells, *seeds* 0.6–0.7 cm diam., reniform, reddish brown, laterally depressed; dorsal ridges obvious, 3, continuous, monomorphic, more than 1 mm thick, 0.5 mm high, smooth on both sides (sometimes with a few warts).

Phenology. Flowering from May to September; mature fruits are known only in August.

Distribution and habitat. *Dracontium longipes* is limited to the area near the border of Acre, Brazil, and Madre de Dios, Peru. It occurs in *Tropical moist forest* (T-mf) and *Premontane wet forest* (P-wf) life zones (Holdridge et al., 1971), at elevations of 150 m.

Discussion. *Dracontium longipes* is easily confused vegetatively with *D. plowmanii* and *D. spruceanum*, but is distinguished from those species by having a cymbiform rather than an erect or arching spathe. *Dracontium plowmanii* also differs from *D. longipes* in having a spathe with undulate or lobed margins and small seeds with a single continuous ridge. In contrast, the spathe of *D. longipes* has straight margins and the seeds have three obvious dorsal ridges. *Dracontium spruceanum* differs in having seeds with more than three dorsal ridges.

Additional specimens examined. BRAZIL. **Acre:** INCRA at ca. 4 km S of main rd. Cruzeiro do Sul to Rio Branco, *Croat 62349* (MO); Rio Juruá Miry, *Ule 5272* (B); Vista Alegre, Rio Jurua Miry, *Croat 85460* (HPZ); Rio Juruá to Mirim at Porangaba, *Maas et al. 13201* (NY); Santa Rosa, Rio Purus, *Daly et al. 10000* (NY). PERU. **Madre de Dios:** Manu Park, Cocha Cashu, Río Manu, *Foster 6978* (F, MO, QCA), *Núñez et al. 14420* (MO).

13. Dracontium margaretae Bogner, Aroideana 4: 87, figs. 1–6. 1981. TYPE: Brazil. Mato Grosso do Sul: Parque Indigena do Xingu, Posto Leonardo, 23 Nov. 1973, *M. Emmerich 4053* (holotype, R!; isotype, M!). Figure 16.

Dracontium lineare G. S. Bunting & Tillett, Phytologia 64: 464. 1988. Syn. nov. TYPE: Venezuela. Apure: Achaguas y Rómulo Gallegos, Río Capanaparo, poco arriba de El Porvenir, en las cercanías del Hato San Joaquín, en varios pequeños asentamientos Pumé Santa Bárbara, Los Mangos, Las Maravillas y Las Campanas, 6°48–52′N, 68°45–48′W, 80 m, 10 July 1986, *T. Gragson & G. Gragson 13* (holotype, US!; isotypes, MYF not seen, MCA not seen, UCV not seen).

Tuber hemispherical or irregular-shaped, 10–12 cm diam., 8–10 cm thick, flat or slightly sunken above, rounded or flat and whitish to light brown below, 10–15 cm below ground level; tubercles abundant, cylindrically elongated, 0.5–0.8 cm diam., 1–2.5 cm long, borne around the periphery and the side of tuber. Roots whitish sometimes tinged brown, to 3.5 mm diam.; *cataphylls* 1 or 2, 10–30 cm long, 2–4 cm wide, pinkish or reddish brown, 5–15 cm long above ground. *Leaves* solitary or sometimes 2 or more per tuber; *petioles* 0.3–0.9 m long above ground, 2–3 cm diam. at midpoint, light green (in upper half) or brown-green (in lower half), weakly mottled, smooth (often); juvenile blade linear or trifid; mature *blade* ascending to 45° to the petiole, 0.5–0.7 m diam., thinly coriaceous, never fenestrated, never variegated, without raphide cells or dark markings, semiglossy and medium green above, semiglossy and medium green below;

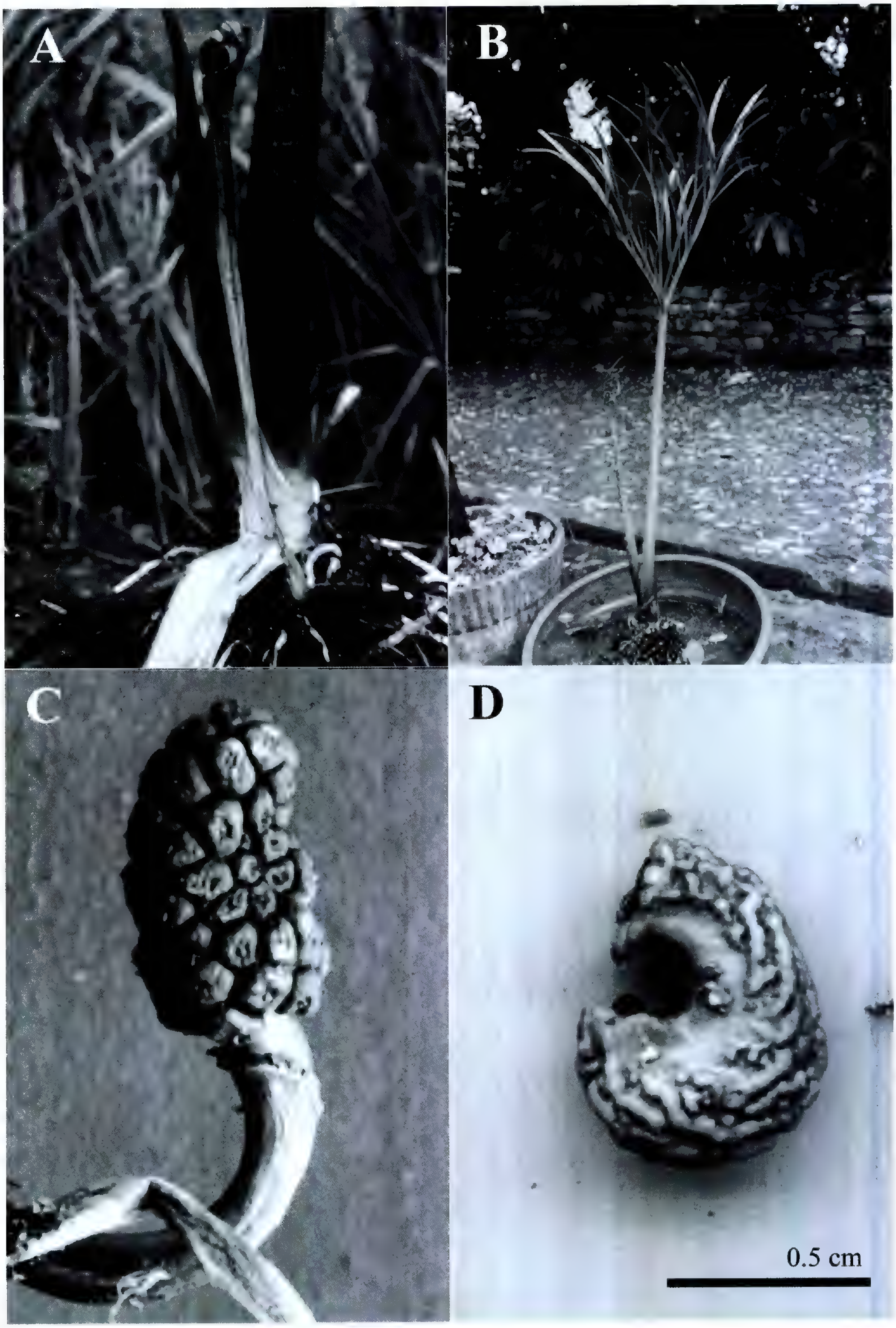

Figure 16. A–D. *Dracontium margaretae*. —A. Tuber, petioles, cataphylls, and an inflorescence (*Catharino 1832*). —B. Potted plant with tuber bearing tubercles, a fully formed leaf, and an opening leaf (*G. Zhu 1533*). —C. Tuber with infructescence, type specimen (*Emmerich 4053*). —D. Seed in side view (*T. G. Gragson 4*).

middle division twice trichotomously branched, 37–45 × 30–40 cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 35–45 × 30–40 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each usually consisting of a single segment; leaf segments often entire, linear, less than 1 cm wide on each side of the major ribs, linear, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments; apices acuminate; *ultimate segments* 10–20 cm long, free from penultimate segments; other segments 10–30 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments absent, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins conspicuous above and weakly raised below; *bracteoles* 2 or 3, 6–25 cm long, 1–3 cm wide, dark brown or pinkish, the longest one shorter than the peduncle, reaching the spathe. *Inflorescence* solitary, appearing after new leaf; *peduncle* 3–10 cm long above ground, 0.5–1 cm diam. at midpoint, often almost completely subterranean (or under water), scarcely mottled, whitish tinged pink, smooth; *spathe* 4–8 cm long, 1–2.5 cm wide, cymbiform, cucullate, arching 90° (or more), apex acuminate; inner surface covered with dense, translucent scales to 1 mm long, olive-brown, with translucent area obscure; outer surface maroon tinged brown, matte; margins entire, slightly overlapping at the base; veins obscure inside and raised outside, conspicuously darker or paler than the spathe; *spadix* exposed, stipitate, cylindric, brown, 1.3–2 × 0.6–1 cm at anthesis, often with several appendages at apex; stipe 0.4–0.5 × 0.3–0.4 cm at anthesis. Flower tepals 5 to 6, 1–2 mm long, 0.5–1 mm wide, brownish purple; stamens 6; filaments 1–2 mm long; anthers 0.5 mm long, completely exserted; ovary bilocular, pale green; stigma 2-lobed; style 1–2 mm long above tepals, brownish purple, persistent. *Infructescence* with spadix 2–4 × 1.5–2.5 cm in fruit; *berries* 2- or 3-seeded, 0.5–0.9 × 0.7–0.8 cm, globose or subglobose, 3- to 6-angular, apically rounded or subtruncate, drying ca. 7 mm thick, 2- or 3-lobed; young berries medium green; mature berries reddish or purplish red, with abundant raphide cells; seeds 0.4–0.6 cm diam., reniform, light brown, laterally depressed, 2.2–2.3 cm thick; sparsely beset with irregular warts dorsally, dorsal ridges obscure.

Phenology. Flowering from May to November; mature fruits are known only in May.

Distribution and habitat. *Dracontium margaretae* is known only from a few localities in Brazil (Mato Grosso do Sul), Paraguay, and Venezuela (Apure and Guárico). It occurs in seasonal swamps in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at elevations of ca. 100 m.

Discussion. *Dracontium margaretae* is an atypical member of the genus, recognized by its linear blade segments and by occurring in seasonally swampy habitats. Other distinguishing features include the linear or trifid juvenile leaf blades and tubercles borne at the apex and sides of the tuber. It is confused with no other species. This species grows well as an aquatic in cultivation.

The species described under the name *Dracontium lineare* G. S. Bunting & Tillett (Bunting, 1988) is identical to *D. margaretae*; therefore, the former name is treated as a synonym of the latter.

Additional specimens examined. BRAZIL. Palmas, Estrada para Tocantinia, *Gonçalves 97* (UB). **Mato Grosso do Sul:** Parque Indigena do Xingu, Posto Leonardo, *M. Emmerich 4598* (K, M); Puerto João André-Brasilândia, ca. 7 km before Brasilândia, *Catharino et al. 1832* (SP). PARAGUAY. Estero Laguna, Est. Keicus, *Hassler 10960* (G, MO). VENEZUELA. **Apure:** Dist. Achaguas y Rómulo Gallegos, Río Capanaparo, El. Porvenir, *Gragson & Gragson 4* (US), *13* (MYF, VEN). **Guárico:** Santa Rita, near the rd. to Cabruta, *Susach 251* (VEN), *Trujillo 12633* (MY).

Cultivated plants. Brazil. Mato Grosso do Sul, vouchered as *Catharino 1832*, cult. at Jardim Botânico de São Paulo, *G. Zhu 1533* (MO, SP).

14. Dracontium nivosum (Lem.) G. Zhu, World Checklist & Bibliogr. Araceae, 301. 2002. *Amorphophallus nivosus* Lem., Ill. Hort. 12: 1, fig. 424. 1865. TYPE: figure 424 in Ill. Hort. 12: 1865 (lectotype, designated here). Figure 17.

Amorphophallus papillosus hort. ex Rafarin, Rev. Hortic. 43: 476, fig. 65. 1871. TYPE: figure 65 in Rev. Hortic. 43: 477, 1871 (lectotype, designated here).

Tuber hemispherical or rounded, 6–12 cm diam., 4–8 cm thick, flat above, rounded and white to brown below, 6–27 cm below ground level; tubercles few, rounded, 0.8–1.5 cm diam., borne around the periphery of tuber, roots white, 2–3 mm diam.; *cataphylls* 1 to 3, 9–28 × 2–3 cm, light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–2 m long above ground, 2.5–3 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile

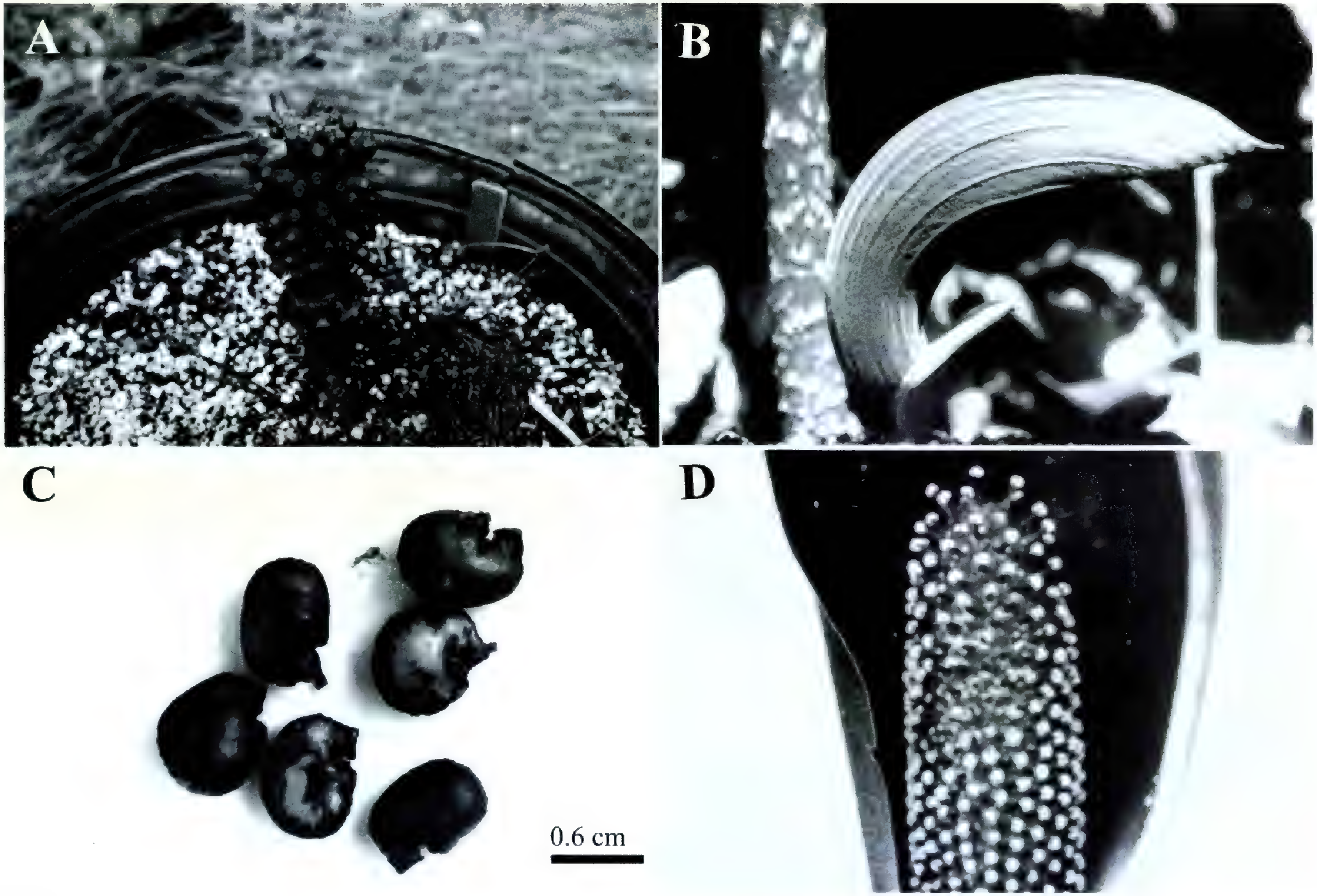

Figure 17. A–D. *Dracontium nivosum*. —A. Cultivated plant at John Banta's nursery. Immature infructescence. —B. Cultivated plant at John Banta's nursery. Flowering plant at anthesis. —C. (*Huber 3667*). Seeds in side view. —D. (*Hetterscheid AR-017*). Inflorescence with spathe cut open to expose spadix. Photo by W. Hetterscheid.

blade sagittate, or sagittately lobed; mature *blade* spreading horizontally, 0.8–1 m diam., often thinly coriaceous, rarely fenestrate, sometimes variegated (along the veins), without raphide cells or dark markings, matte and medium green above, matte and pale green below; *middle division* twice trichotomously branched (often), 30–45 × 20–40 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 28–45 × 30–45 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate or oblanceolate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate; *ultimate segments* 6–8 cm long, often confluent with penultimate segments; other segments 5–12 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, with spiny projections; tertiary veins obscure above, or conspicuous below; *bracteoles* 3 or 4, 2–28 × 1–2 cm wide, light brown, the longest one ± as long as the peduncle, reaching the spathe. *Inflorescence* solitary, appearing before new leaf; *peduncle* 0–2 cm long above ground, 1–1.5 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, whitish tinged pink, smooth; *spathe* 28–35 × 6–10 cm, cymbiform, cucullate, arching to 45°, apex acuminate; inner surface semiglossy, maroon, with translucent area obscure; outer surface maroon, matte; margins entire, broadly overlapping in the lower half; veins obscure inside and raised outside, similar to the spathe in color; *spadix* hidden, stipitate, cylindric, purple or brown-purple, (3–)5–6.5 cm long, 1.2–1.5 cm diam. at anthesis, never with appendages at apex; stipe 0.6–1.2 cm long, 0.5–1 cm diam. at anthesis. Flower tepals 5 to 8, 2.5–3 mm long, 1–2 mm wide, purple; stamens 6 to 8; filaments 2–2.5 mm long; anthers 0.5–1 mm long, slightly exserted; ovary 3-locular; stigma 3-lobed; style 4–5.5 mm long above tepals, purple, persistent. *Infructescence* with spadix 12–18 cm long, 3–3.5 cm diam. in fruit; *berries* 3- or 4-seeded or sometimes 2-seeded, 0.8–1 cm diam., 0.8–1 cm thick, subglobose, 3- to 6-angular, apically truncate; mature berries orange (tinged red), with abundant raphide cells; *seeds* 0.5–0.7 cm diam., reniform or rounded, light brown, laterally raised; dorsal ridges obvious, 3, continuous, less than 0.5 mm thick, 0.1 mm high, finely decorated with small cells on both sides.

Phenology. Flowering May to July; mature fruits from December to March.

Distribution and habitat. *Dracontium nivosum* is endemic to Pará and Maranhão, Brazil. It occurs in *Tropical moist forest* (T-mf) and *Tropical wet forest* (T-wf) life zones (Holdridge et al., 1971) at elevations of 30 to 150 m.

Local names. "Tajá de cobra" (*Black 47-2084*, MG); "jararaca-taja" (Schott, 1865: 73).

Discussion. *Dracontium nivosum* is characterized by its subterranean peduncle with a strongly hooded and cymbiform spathe, a spathe much larger than that of any other member of the genus possessing subterranean peduncles. Other species with peduncles at least sometimes subterranean such as *D. amazonense*, *D. bogneri*, *D. dubium*, *D. grayumianum*, *D. polyphyllum*, *D. prancei*, *D. purdieanum*, *D. soconuscum*, and *D. ulei* have spathes only 3–15(18) cm long, whereas the spathe is 28–35 cm long for *D. nivosum*. Other species that, like *D. nivosum*, have the spadix hidden at anthesis owing to the broadly overlapping spathe base include *D. amazonense*, *D. bogneri*, *D. prancei*, and *D. ulei*, but none of them have ranges overlapping that of *D. nivosum*.

Common names attributed to snakes obviously refer to the reptilian pattern exhibited by the petioles. Perhaps for the same reason many species of *Dracontium* are used by native populations for snakebite remedies (Croat, 1994). This species is known in cultivation at the Instituto Agronomico do Norte (IAN) at Belém, Pará State, Brazil. A plant of the species, collected from Santarem, Brazil, flowered in John Banta's nursery in Florida in 1993.

Since no type was chosen for *Amorphophallus nivosus* Lem., the only plate from the protologue (Ill. Hort. 12: 1, fig. 424. 1865) is designated here as a lectotype for the name. Two figures of this species appeared earlier before its publication under the name *D. polyphyllum* (Bot. Reg. 9: fig. 700 A&B, 1823).

Apparently based on a cultivated plant, another name, *Amorphophallus papillosus* hort. ex Rafarin (Rev. Hortic. 43: 476, 1871), was published for the same species. In the protologue of *A. papillosus*, no type was designated and one illustration (fig. 65 in Rev. Hortic. 43: 477, 1871) was included with a caption mistakenly noted as *A. nivosus*. For the integrity of nomenclatural citation, the illustration (fig. 65 in Rev. Hortic. 43: 477, 1871) is designated here as a lectotype for the name *A. papillosus*.

Dracontium nivosum was previously noted (as nomen nudum) to occur in Peru (Vásquez et al., 2002 [2003]).

Additional specimens examined. BRAZIL. **Maranhão:** Monção, P. I. Guajá, Río Turiaçu, Guajá Indianas, *Balée 3476* (NY). **Pará:** "Taperinha, bei Santarem," 16 June 1927, *Ginzberger 3109* (WU); Barcarena, Itupanema, *Gély 234* (MG); Mpo. Tucuruí, Río Tocantins, 1–5 km from Represa Tucuruí, *Plowman et al. 9895* (MG); Rio Cupari, Ingatuba capoeira, *Black 2084* (IAN, RB); BR-423, *Machiel & Rosário 534* (MG); Vigia, Campina do Palha, *Black 18814* (IAN); Paraenfis, 1911, *Martius 282* (M); Belém-São Caetano, km 12, *Lobato et al. 60* (MG).

Cultivated plants. Brazil. Para, Belém, Museu Paraense Emilio Goeldi, Botanical Garden, May 1901, *Huber 2036, 3667* (MG); Instituto Agronomico do Norte (IAN) at Belém, *Lima 108* (IAN, MG), *Pires 6594* (IAN).

15. Dracontium peruvianum G. Zhu & Croat, sp. nov. TYPE: Peru. Loreto: Maynas, Allpahuayo, 4°10′S, 73°30′W, 150–180 m, 4 Dec. 1990, *R. Vásquez & N. Jaramillo 15226* (holotype, MO). Figure 18.

Herba usque plus quam 6 m alta; petiolus 2–6 m longus; lamina 0.6–1 m longa, 0.6–0.9 m lata; pedunculus 60–115 cm longus, 1.5–6 cm diam.; spatha (25)30–50 cm longa, 6–10 cm lata; extus impolita, purpurea; intus velutina, purpurea; spadix 8–10.5 cm longus, 1–1.3 cm diam.; baccae 0.7–1 cm diam.; semina fusca, 0.7–1 cm diam.

Tuber hemispherical, 10–30 cm diam., 8–15 cm thick, flat above, rounded and white to brown below, 15–45 cm below ground level; tubercles few, rounded or cylindrically elongated, borne around the periphery of tuber; roots white, to 0.4 mm diam.; *cataphylls* 1 or 2, 10–50 × 2.5–4 cm, reaching or surpassing ground level. *Leaves* solitary; *petioles* 2–6 m long above ground, 3.6–5 cm diam. at midpoint, dark green (paler toward the apex), contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually with spiny projections (especially in upper half or at the apex); juvenile blade sagittate, or sagittately lobed; mature *blade* spreading horizontally, 1.2–2 m diam., thinly coriaceous, rarely fenestrate or sometimes fenestrate throughout the blade (in young leaves), never variegated, lacking raphide cells or dark markings, semiglossy and dark green above, matte and medium green below; *middle division* twice trichotomously branched, 60–100 × 60–90 cm, with terminal subdivision never divided into sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 55–95 × 55–90 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, at least some of the basal segments free from each other, without contrastingly smaller rounded or triangular segments; apices acute or acuminate; *ultimate segments* 20–27 cm long, often confluent with penultimate segments; other segments 10–15 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and weakly raised below; *bracteoles* 1, 15–50 cm long, 2–4 cm wide, light brown, the longest one much shorter than the peduncle, confined at the base of the peduncle. *Inflorescence* solitary, appearing before new leaf; *peduncle* 60–115 × 1.5–6 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, with irregular protuberances in lower half and spiny projections (in upper half, especially at the apex); *spathe* (25–)30–50 × 6–10 cm, cymbiform, noncucullate, erect or slightly arching, apex acuminate; inner surface semiglossy, maroon, with translucent area obvious, 5–8 cm high, shorter than spadix; outer surface maroon tinged brown, matte; margins entire, slightly overlapping at the base; veins obscure inside and raised outside, conspicuously darker or paler than the spathe; *spadix* hidden, stipitate, cylindric, brown or brown-purple, 8–10.5 × 1–1.3 cm at anthesis, never with appendages at apex; stipe 0.5–2 × 0.5–1 cm at anthesis. Flower tepals 5 to 7, 1–2 × 1–2.5 mm, light brown or brown-purple; stamens 7 to 11; filaments 1–1.5 mm long; anthers 0.5 mm long, hidden; ovary 3-locular, pale green; stigma 2- or 3-lobed; style 1–1.5 mm long above tepals, brownish purple, persistent or not. *Infructescence* with spadix 23–35 × 2.8–3 cm in fruit; *berries* 1- to 3-seeded, 0.5–1 cm diam., 0.7–1 cm thick, obliquely obovoid or globose, apically rounded or subtruncate; young berries medium green; mature berries orange, without reddish dots and raphide cells; *seeds* 0.7–1 cm diam., rounded, dark brown, laterally raised; dorsal ridges obvious, 3, continuous or rarely strongly interrupted, with the central ridge contrastingly raised, more than 1 mm thick, 1–2 mm high, smooth on both sides.

Phenology. Flowering April to November; mature fruits July to March, with a peak in December.

Distribution and habitat. *Dracontium peruvianum* is known only from Amazonian Peru and Brazil. It occurs in *Tropical moist forest* (T-mf), *Premontane*

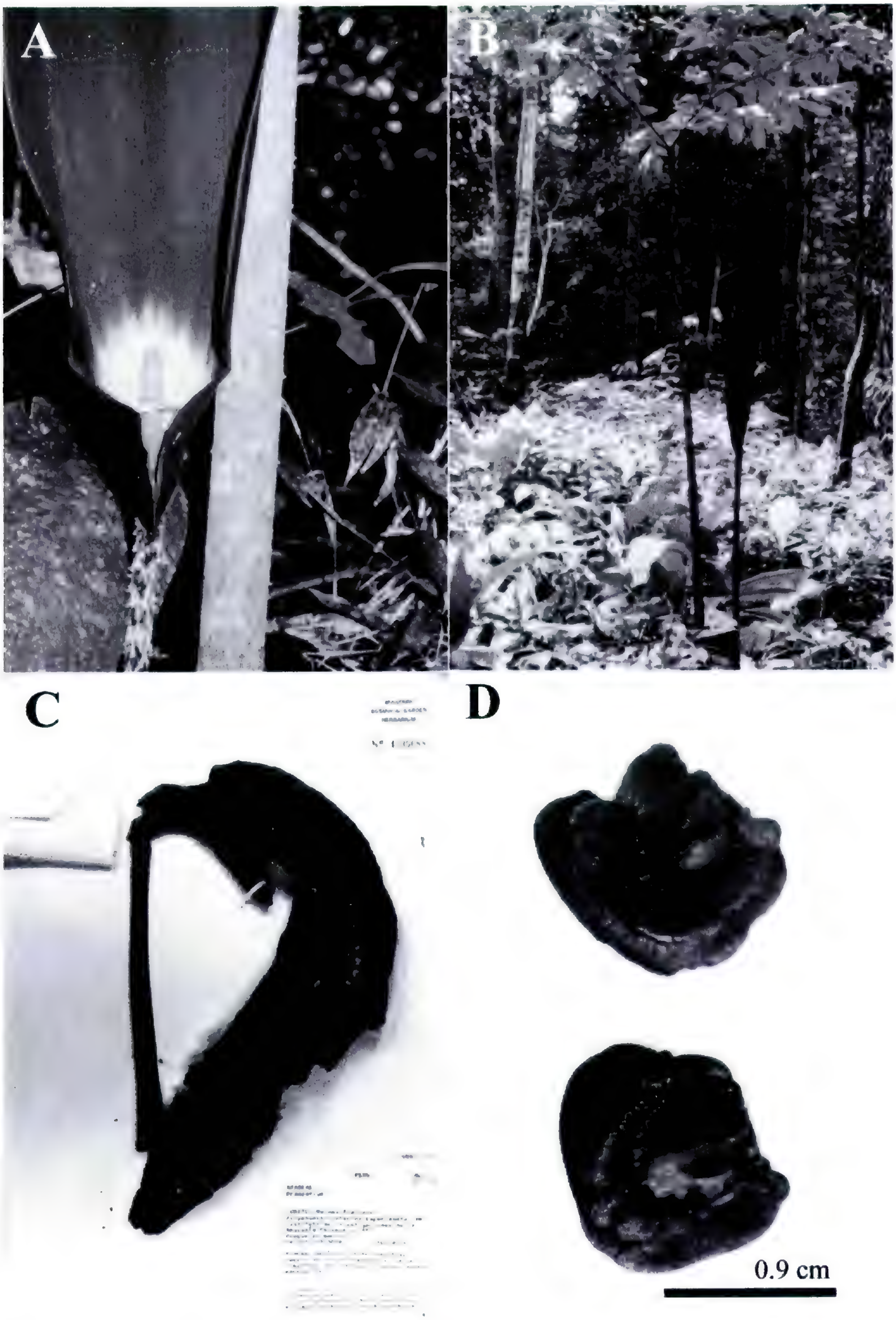

Figure 18. A–D, *Dracontium peruvianum*. —A. Inflorescence in Ucayali Department, Peru. Photo W. Staeck. —B. Flowering plant in Parque Nacional Alexander von Humboldt, near Pucalpa, Ucayali Department, Peru. Photo by A. Salazar. —C. Infructescence with persistent spathe type specimen (*Vásquez & Jaramillo 15226*). —D. Seeds in lateral view (*Gentry & Daly 18798*).

moist forest (P-mf), and *Tropical montane moist forest* (TM-mf) life zones (Holdridge et al., 1971), at elevations of 180 to 900 m.

Local names. "Jergón sacha" (*Plowman & Schunke 11536*, MO).

Discussion. *Dracontium peruvianum* has the longest leaves of any species in the genus, up to 6 m long. The inflorescences of this species are superficially similar to those of *D. pittieri*, but are distinct by the more elongate fruiting spadix (to 23–35 cm long vs. 10–20 cm long for *D. pittieri*), more strongly ridged seeds (vs. less ridging in *D. pittieri*), and basal leaf segments that usually are free from the rachis.

In having such a long peduncle *D. peruvianum* is similar to *D. asperispathum*, *D. croatii*, *D. grandispathum*, *D. longipes*, *D. plowmanii*, and *D. spruceanum*, but only *D. croatii*, *D. longipes*, and *D. pittieri* also have a cymbiform spathe that is not differentiated into a proximal tube portion and a distal lamina. *Dracontium croatii* and *D. pittieri* differ in having the spathe obtuse at the apex (vs. acuminate for *D. peruvianum* and *D. longipes*). *Dracontium longipes* differs from *D. peruvianum* in having a much shorter infructescence (only 4–5 cm long vs. 23–35 cm long for *D. peruvianum*).

Paratypes. BRAZIL. **Amazonas:** Rio Juruá basin, near mouth of Rio Embira (tributary of Rio Tarauaca), *Krukoff 4987* (GH, NY). PERU. **Huánuco:** Pachitea, Honoria, Río Pachitea, *Schunke-Vigo 1775* (F); Tingo María, *Gentry & Daly 18798* (F, MO). **Loreto:** Río Amazonas, Isla de Iquitos, *Rimachi 5304* (IBE); Nauta, *Vásquez & Jaramillo 8562* (MO); Fernando Lores, Quebrada Tamshiyacu, *Grández et al. 2629* (MO), *Rimachi 4043* (IBE); Iquitos, *L. Williams 7916* (F); Río Itaya just below mouth of Río Ucayali, *Gentry et al. 30026* (MO); San Antonio, Río Itaya, *Vásquez & Jaramillo 3598* (MO); Río Ucayali, Santa Rosa, *Jong 20* (MO); Yurimaguas, NCSU Exp. Station, near headquarters, *Gentry et al. 52159* (MO); lower Río Huallaga, *L. Williams 4631* (F); San Salvador on the Amazon River, *L. Williams 1561* (F). **Pasco:** Palcazu Valley, Iscozacin, above PEPP Project Camp, *Salick 7370* (MO). **San Martín:** 12 km W of Tocache Nuevo, *Gentry et al. 25597* (MO); Tarapoto-Yurimaguas, km 40, trail to Río Tiriyacu and Río Cashiyacu, *Knapp & Mallet 7210* (MO); Tocache Nuevo, Tocache Nuevo-Puerto Pizana, km 23, Río Cañuto, *Plowman & Schunke 11536* (F, MO, SEL); Lamas Convento, Tarapoto-Yurimaguas, km 68, *Alcorn & Mallet 8* (MO); Mariscal Cáceres, Dtto. Tocache Nuevo, Quebrada de Huaquisha, *Schunke 7140* (MO); Puerto Huicte, Río Huallaga, *Schunke 6428* (UCLA); Yorongos-La Florida near Rioja, *van der Werff et al. 16538* (AAU, B, CAS, K, MEXU, MO, US, USM).

Cultivated plants. Peru. Humboldt National Park between Pucallpa and Tingo María, collected by Angel Salazar, cult. at MBG, *T. B. Croat 53539* (MO).

16. Dracontium pittieri Engl., Anales Inst. Fis.-Geogr. Nac. Costa Rica 9: 209. 1896. TYPE: Costa Rica. Puntarenas: Río Naranjo, 200 m, *H. Pittier & A. Tonduz 7515* (lectotype, designated here, CR!; isotypes, B!, BR!). Figure 19.

Tuber hemispherical, 14–20 cm diam., 6–8 cm thick, flat above, rounded and white to brown below, 20–40 cm below ground level; tubercles abundant, irregular-shaped, 0.3–1.5 cm long, borne around the periphery of tuber; roots white, to 3 mm diam.; *cataphylls* 3 to 5, 4–40 × 4–7 cm, light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1.8–4 m long above ground, 5–8 cm diam. at midpoint, dark green or brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth or usually with spiny projections; juvenile blade sagittate, or sagittately lobed; mature *blade* spreading horizontally, 1.2–2 m diam., subcoriaceous or thinly coriaceous, rarely fenestrate, never variegated, with abundant raphide cells (sometimes), glossy and dark green above, semiglossy and medium green below; *middle division* 3 or more times trichotomously branched, 80–120 × 50–100 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 or more times dichotomously branched, 70–120 × 55–90 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent, each consisting of many segments; leaf segments bilobed or trilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate or lanceolate-ovate or triangular, mostly confluent with each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices narrowly acuminate, or caudate; *ultimate segments* 10–20 cm long, confluent with penultimate segments; other segments 10–30 cm long; penultimate segments confluent with the subterminal sections; medial segments confluent with the basal subdivisions; basal segments present, confluent with each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins obscure above, or conspicuous below; *bracteoles* 3 or 4, 4–40 cm long, 5–7 cm wide, pinkish, the longest one much shorter than the peduncle, confined at the base. *Inflorescence* solitary, appearing before new leaf; *peduncle* 150–250 cm long above ground, 4–6 cm diam. at midpoint, more than half as long as the petiole, mottled similar to petiole but deeper in color, dark green, smooth or with irregular protuberances; *spathe* 30–50(70) cm long, 8–12 cm wide, cymbiform, non-cucullate, erect or slightly

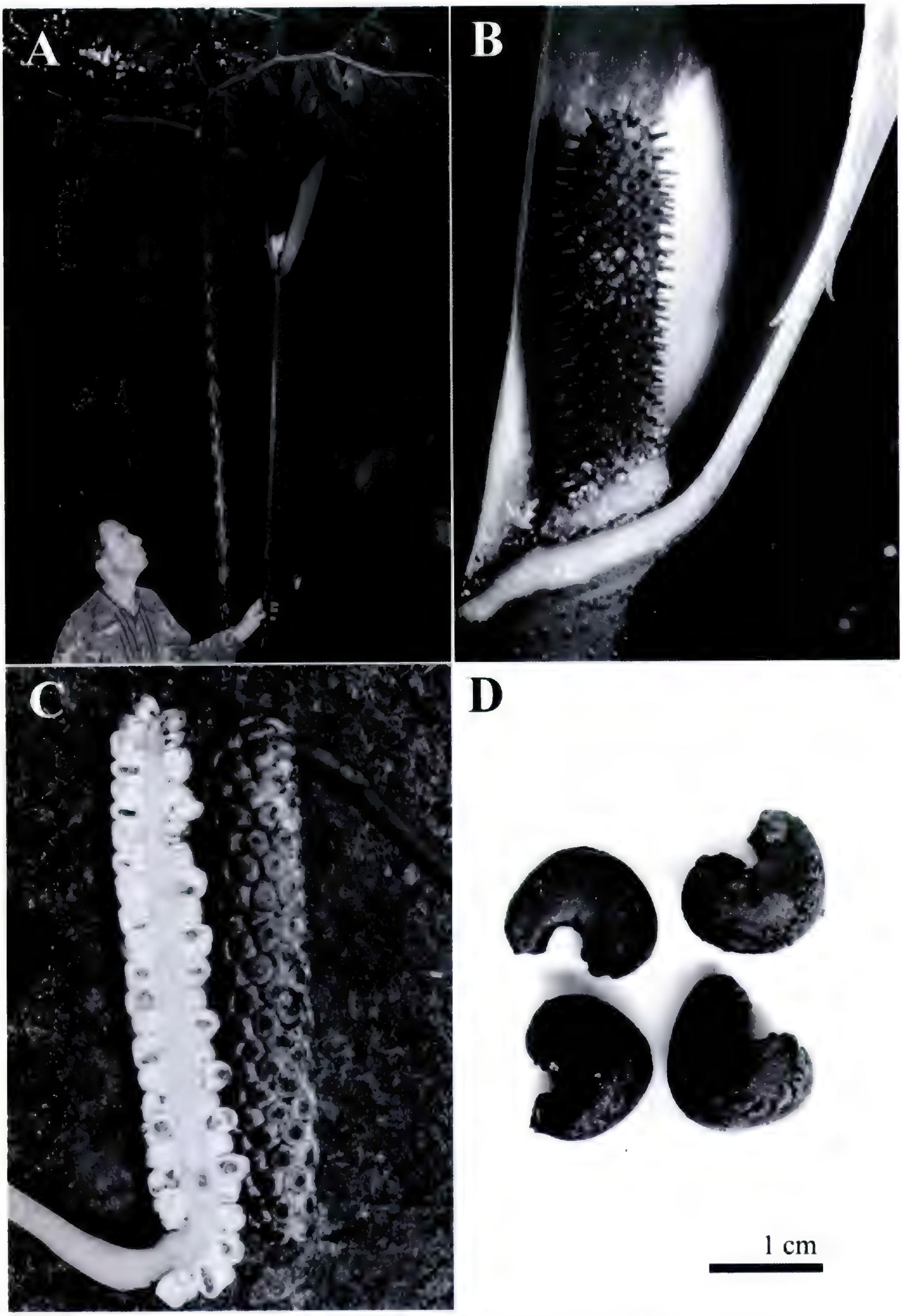

Figure 19. A–D, *Dracontium pittieri*. A–C, (*Croat & Hannon 79217*). —A. Habit of flowering plant with Dylan Hannon. —B. Close-up of spathe with one side removed to expose spadix. —C. Infructescence with premature berries. —D. (*Burger 12266*). Seeds in side view.

arching, apex obtuse; inner surface semiglossy, maroon or olive-brown or red-purple, with translucent area obvious, (5)10–17 cm high, 1.5 to 3 times longer than spadix; outer surface maroon, matte; margins entire, hardly overlapping at the base; veins obscure inside or raised outside, similar to the spathe in color; *spadix* exposed, sessile, cylindric, brown-purple (tinged green) or purple, 4–9 × 1–1.5 cm at anthesis, never with appendages at apex. Flower tepals (4)5 or 6(9), 3–4 mm long, 1–1.5 mm wide, brownish purple or dark purple; stamens 12 to 15; filaments 2–3 mm long; anthers 1 mm long, slightly exserted; ovary bilocular, whitish; stigma (2)3(4)-lobed; style 3–4 mm long above tepals, purple, persistent. *Infructescence* with spadix 10–20 cm long, 3–4 cm diam. in fruit; *berries* 2-seeded, 0.6–1.2 cm diam., 0.9–1.3 cm long, subglobose, 3- to 6-angular, apically truncate; young berries medium green; mature berries orange, with abundant raphide cells; *seeds* 0.9–1.1 cm diam., reniform or triangular, light brown, laterally flattened; dorsal ridges obvious, 1, continuous, more than 1 mm thick, 0.5–1 mm high, warty along both sides, appearing as strongly reduced lateral ridges.

Phenology. Flowering from May to November; one inflorescence was also collected in February; mature fruits in November and February.

Distribution and habitat. *Dracontium pittieri* is endemic to the Pacific slope in Puntarenas Province and adjacent San José Province in Costa Rica. It occurs in *Tropical moist forest* (T-mf) and *Premontane moist forest* (P-mf) and *Tropical wet forest* and transition forest to *Premontane wet forest* life zones (Holdridge et al., 1971). It is often found along river banks, roadsides, secondary growth, and other disturbed areas, at elevations of 30 to 1000 m.

Discussion. *Dracontium pittieri* is characterized by having the longest peduncles in the genus. It is easily confused with *D. gigas* in sterile condition, but differs strikingly in inflorescence morphology (see also discussion of *D. gigas*). *Dracontium gigas* has a large spathe and a short peduncle, which is always less than twice as long as the spathe, whereas *D. pittieri* has a much longer peduncle, 5 to 8 times longer than the spathe. The spathe of *D. gigas* is more or less hooded at the apex, with the margins broadly overlapping and completely covering the spadix. The spathe of *D. pittieri* is open at the apex with the margins scarcely overlapping, such that the spadix is exposed. The translucent area at the base of the inner spathe surface extends much higher than the spadix in *D. pittieri*, while it never exceeds the height of the spadix in *D. gigas*.

Aside from the fact that they are widely separated geographically, *D. pittieri* could also easily confused with *D. peruvianum*; they differ, however, in the features of infructescences, seeds, and leaf blades (see discussion of *D. peruvianum*). A few plants of this species have been brought into cultivation in the United States, but no report of flowering is known. Several plants of *D. pittieri* are known from John Banta's Nursery (Alva, Florida).

In the protologue, two specimens, *Pittier & Tonduz 7515* and *Pittier 11985*, were cited without indication of a holotype (Engler, 1896). Therefore, one of them needs to be designated as the holotype. The *Pittier & Tonduz 7515* collection has three duplicates that are deposited in three different herbaria (B, BR, CR) and are in much better condition than the unicate *Pittier 11985*; therefore, the former collection is designated here as lectotype for the name *D. pittieri*. A description of this species was published at a later date (Engler, 1905).

Additional specimens examined. COSTA RICA. **Puntarenas:** Boca Culebra, *Pittier 11985* (CR); Fila de Cal, betw. San Vito & Ciudad Neily, *Grayum et al. 6046* (MO); Cantón de Osa, 2.5 mi. SW of Rincón, *Croat & Grayum 59844* (CM, MO), *Kennedy 1646* (MO); Fila Retinto, cerros N Palmar Norte, *Hammel 17713* (CR); Rancho Quemado, Rincón, *Marín 285* (CR, MO), *Quesada 259* (CR, INB, MO); above Palmar Norte, *Allen 5318* (EAP, MO, US), *Croat 35104* (CM, F, MO); vic. Rincón, *Hammel et al. 15204* (MO); 5 km W of Rincón de Osa W of airfield, *Burger & Stolze 5551* (F, NY); Quebrada Orito & Quebrada Baneguitas, *Herrera 4529* (MO); Corcovado Nat. Park, Sirena, *Liesner 2867* (CR, MO); Los Patos Forest, *Kernan & Phillips 648A* (MO); Los Patos, Cerro de Oro, *Aguilar & Guzmán 2849* (CR); Coto Brus, Sabanillas de Limoncito, *Gómez 22029* (B, F, K, RSA, US); Esquinas forest, along Panamerican Hwy., *McAlpin 85-34* (SEL); Finca El Edén, km 183, R 2, E of Santa Marta, *Gómez 22935* (CM, MO); Golfito-San Isidro de General, *Kress 76585* (DUKE, F); E of Quepos, *Burger et al. 10587* (F, PAM); Río Agua Buena, 4 km above airport, *Liesner 2017* (MO); Río Naranjo, near Londres & Villa Nueva, *Burger et al. 12266* (F); vic. of Boscosa, Aguabuena, *Croat & D. Hannon 79217* (MO, NY, WU); Golfito, PN Corcovado, *Angulo 273* (INB, MO). **San José:** *R. Ocampo S. 2573* (CR); La Cangreja, Cerros de Puriscal, Santa Rosa de Puriscal, *Morales 546* (CR); Playa, Dominical/Baru/Tinamastes, along rd. to San Isidro del General, *Burger & Baker 10131* (F, MO).

17. Dracontium plowmanii G. Zhu & Croat, sp. nov. TYPE: Peru. Cuzco: Paucartambo, Pilcopata, Villa Carmen, 720 m, 7 Feb. 1975, *T. Plowman & W. Davis 5054* (holotype, GH!; isotype, US!). Figures 1A, 20.

Petiolus 1–2 m longus; lamina 45–55 cm longa, 40–55 cm latis; pedunculus 29.5–70 cm longus, 1–2 cm diam.; spatha 13–20 cm longa, 2.5–3.5 cm lata, cucullata vel non cucullata basi; extus impolita, purpurea; intus velutina, purpurea; spadix 3–4.9 cm longus, 0.8–1.2 cm

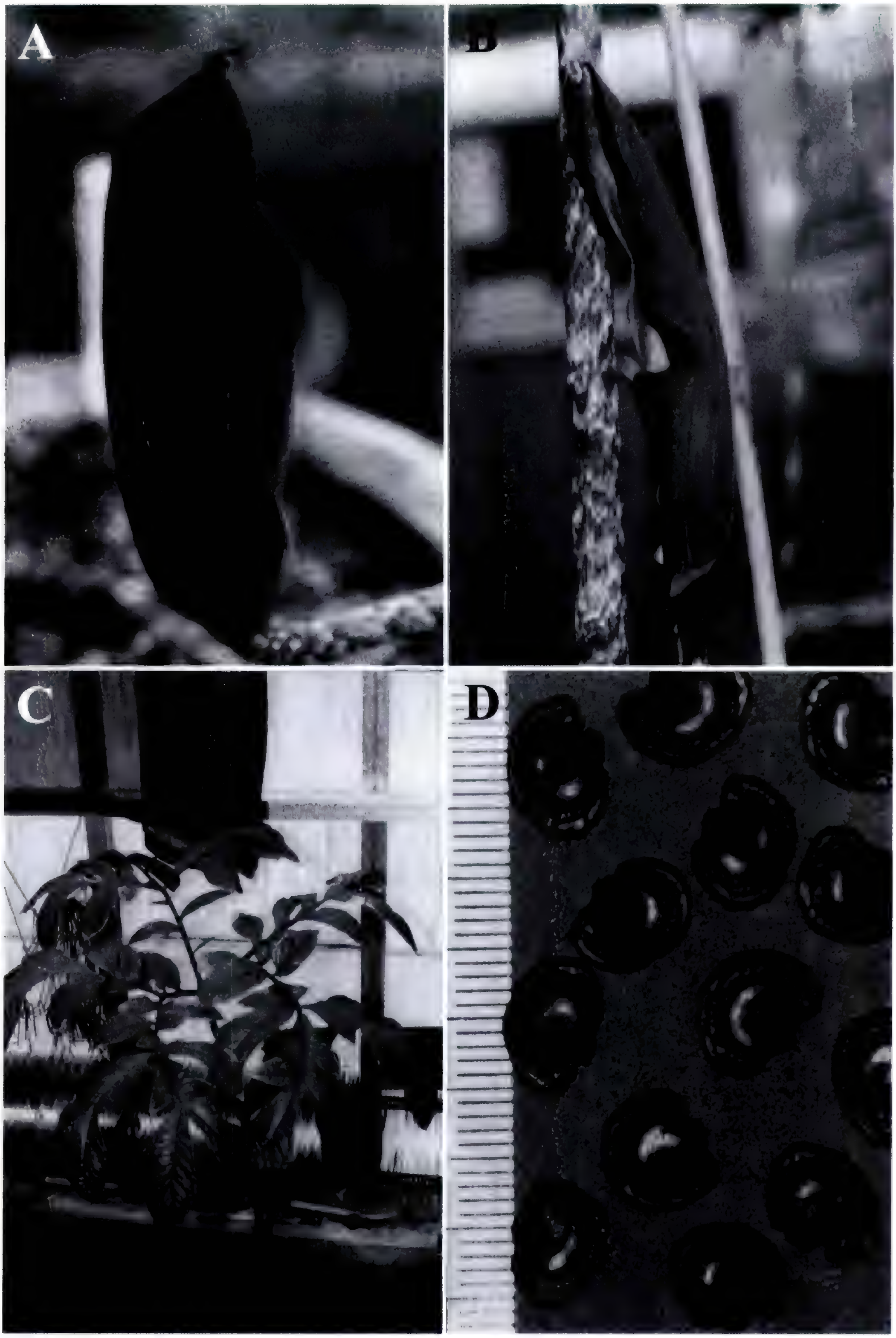

Figure 20. A–D. *Dracontium ploemanii*. Photos A–C by P. Schmidt. —A. (Selby Gardens 76-575). Inflorescence (*G. Zhu 1446*). B, C, (Selby Gardens 77-2421). —B. Spathe in side view with petiole. —C. Leaves of potted plant. —D. Seeds in lateral view. Note: each line on left of photo represents 1 mm (*Cornejo 2049*).

diam.; tepala 4–6; baccae 0.7–1 cm diam.; semina brunneola, 0.4–0.6 cm diam.

Tuber hemispherical, 10–20 cm diam., 6–9 cm thick, flat above, rounded and white to brown below, 5–18 cm below ground level; tubercles few, rounded or cylindrically elongated, 0.5–0.8 cm diam., 0.8–1 cm long, borne around the periphery of tuber; roots white, strong; *cataphylls* 2 to 3, 5.5–18 × 2–4 cm, light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–2 m long above ground, 3–4 cm diam. at midpoint, brownish green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth or usually with spiny projections; juvenile blade sagittate, or sagittately lobed; mature *blades* spreading horizontally, 1–1.2 m diam., thinly coriaceous, sometimes fenestrate throughout the blade, never variegated, without raphide cells or dark markings, glossy and dark green above, semiglossy and medium green below; *middle division* twice trichotomously branched, 45–58 × 40–60 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 45–55 × 40–55 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of a few segments; leaf segments bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, ovate or oblong, at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or acute; *ultimate segments* 10–20 cm long, confluent with penultimate segments; other segments 6.5–19 cm long; penultimate segments confluent with the subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and conspicuous below; *bracteoles* 2 or 3, 4–20 × 2.5–4 cm, pink to dark brown, the longest one much shorter than the peduncle, partially covering the base of the peduncle. *Inflorescence* solitary, appearing before new leaf; *peduncle* 30–70 cm long above ground, 1–2 cm diam. at midpoint, less than half as long as the petiole, mottled similar to petiole but deeper in color, brownish green, smooth; *spathe* (10–)13–20(–28) cm long, (1–)2.5–3.5(–6) cm wide, cymbiform or non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucullate or non-cucullate, erect or slightly arching, apex acuminate; inner surface glossy, purple-red, with translucent area obvious, 3–4 cm high, shorter than spadix or as long as spadix; outer surface maroon, matte; margins wrinkled and sometimes lobed on each side, broadly overlapping at the base; veins conspicuous inside and raised outside, similar to the spathe in color; *spadix* hidden, stipitate, cylindric, brown or brown-purple, 3–4.9 × 0.8–1.2 cm at anthesis, never with appendages at apex; stipe 0.5–0.7 cm long, 0.4–0.6 cm diam. at anthesis. Flower tepals 4 to 6, 1–2.5 × 0.5–1 mm, light brown tinged green or brown-purple; stamens 6 to 9; filaments 0.7–2.2 mm long; anthers 0.5 mm long, slightly exserted; ovary 3-locular, pale green; stigma 3-lobed; style 1–2 mm long above tepals, purple, persistent. *Infructescence* with spadix 6–15 cm long, 2–2.5 cm diam. in fruit; *berries* 1- to 3-seeded, 0.7–1 cm diam., 0.5–0.7 cm thick, subglobose, 4- to 5-angular, apically truncate; young berries dark green; mature berries' color unknown, drying with abundant reddish dots; *seeds* 0.4–0.6 cm diam., reniform, light brown, laterally raised; dorsal ridge 1, obvious, continuous, more than 1 mm thick, 0.5 mm high, smooth on both sides.

Phenology. Flowering from June to August, sometimes in February; mature fruits collected in January and February.

Distribution and habitat. *Dracontium plowmanii* is endemic to Peru, ranging from Junín through Cuzco to the Tambopata area in Madre de Dios. It occurs in *Tropical moist forest* (T-mf) and *Premontane moist forest* (P-mf) life zones (Holdridge et al., 1971), at elevations of 200 to 720 m.

Discussion. *Dracontium plowmanii* is characterized by the often undulate or lobed spathe margins and small seeds with a single continuous dorsal ridge. It is easily confused with *D. spruceanum*, which differs in having larger seeds to 0.7 cm long, with three dorsal ridges, and usually entire and non-wavy spathe margins. It is also superficially similar to *D. longipes*, which differs by having a straight non-wavy margined spathe and seeds that have three obvious dorsal ridges. This species is in cultivation at the Missouri Botanical Garden, Marie Selby Botanical Gardens, and the Dewey Fisk Nursery in Florida.

This new species is named in honor of the late Timothy Plowman, whose numerous collections of Araceae include many live collections introduced to horticulture as well as the type specimen of this species.

Paratypes. PERU. **Cuzco:** Atayala, *Vargas 13433* (US). **Junín:** San Luíz de Shuara, *Plowman & Kennedy*

5654 (F, GH). **Loreto:** Yarina at Río Tapiche, *Vásquez et al. 4841* (MO). **Madre de Dios:** Cocha Cashu, Parque Manu, *Nuñez 1885* (F); Manu, Par. Nac. del Manu on Río Manu, Cocha Cashu Station, *Foster 9558* (F, MO); 12 km E of Puerto Maldonado, *Gentry & Núñez 69383* (MO); Tambopata ca. 30 air km or 70–80 river km SSW of Puerto Maldonado, *Cornejo 1520* (MO, MOL).

Cultivated plants. Peru. Lima, sent by Anderson, cult. Fairchild Tropical Garden, Miami, Florida, (same as Selby 77-2421), *M. Madison 4229* (SEL); Madre de Dios, collected by O. Phillips, 5 Sep. 1994, cult. at MBG, *G. Zhu 1512* (MO); from Selby Gardens (76-575), cult. at MBG, [vouchered as *T. Plowman 5654*], *Croat 73989* (MO), *G. Zhu 1482, 1498* (MO); from Selby Gardens (77-2421), cult. at MBG [vouchered as *M. Madison 4229*], *G. Zhu 1446, 1447, 1480, 1487, 1496, 1496A* (MO); from Selby Gardens (76-575), cult. at MBG [vouchered as *T. Plowman 5654*], *Christenson 1287, 1490, 1491* (MO), *G. Zhu 1466* (MO).

18. Dracontium polyphyllum L., Sp. Pl. 967. 1753, non *Dracontium polyphyllum* Houtt., Handl. Pl.-Kruidk. 11: 199. 1773–1783, hom. illeg. [= *Amorphophallus giganteus* Blume]; nec *Dracontium polyphyllum* Forst. f., Diss. Pl. Esc. 61, n. 29. 1786, hom. illeg. [= *Amorphophallus paeoniifolius* (Dennst.) Nicolson]; nec *Dracontium polyphyllum* Dennst., Schluess. Hort. Malab. 38. 1818, hom. illeg. [= *Amorphophallus dubius* Blume]; nec *Dracontium polyphyllum* A. Cunn. ex A. DC., in DC., Prod. 16(2): 534. 1866, hom. illeg. [= *Bowenia spectabilis* Hook. f.]. TYPE: plate 93 in Herm., Parad. Bat. 1698 (lectotype, designated by Hay (1992: 189)); French Guiana, Saül, 13 Feb. 1993 (*T. B. Croat 74210*) [cultivated plant at MBG], *G. Zhu 1462* (epitype, designated by Zhu & Grayum (1995: 521), MO!). Figures 1B, 1C, 21.

Dracontium asperum K. Koch var. *wallisii* Engl. in Mart., Fl. Bras. 3(2): 126. 1878. Syn. nov. *Amorphophallus wallisii* Regel, Gartenfl. 322. 1861, nom. invalid. TYPE: Brazil. Pará: *Martius s.n.* (holotype, not seen, probably B or M).

Echidnium regelianum Engl., in DC., Monogr. Phan. 2: 286. 1889. Syn. nov. *Dracontium regelianum* (Engl.) Bogner, Aroideana 8: 78. 1985. *Echidnium spruceanum* Regel, Gartenfl. 15: 98, t. 503. 1866, non Schott. TYPE: tab. 503 in Gartenfl., 1866: 98 (lectotype, designated by Bogner (1985: 78)).

Tuber hemispherical or rounded, 6–10 cm diam., 5–8 cm thick, flat above, rounded and white to brown below, 5–15 cm below ground level; tubercles few, cylindrically elongated or irregular-shaped, 0.5 cm diam., 1 cm long, borne around the periphery of tuber; roots white, to 0.3 cm diam.; *cataphylls* 3 to 5, 3–16 cm long, 1–2 cm wide, light brown, reaching or surpassing ground level. *Leaves* solitary or sometimes two or more per tuber; *petioles* 1–2 m long above ground, 2–3.5 cm diam. at midpoint, dark green or brown-green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blade* spreading horizontally, 0.8–1 m diam., papyraceous, sometimes fenestrate, sometimes variegated, with abundant raphide cells (sometimes), glossy and dark green above, semiglossy and medium green below; *middle division* twice trichotomously branched, 50–80 × 50–75 cm, with terminal subdivision consisting of three sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 50–80 × 45–70 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections confluent or free, each consisting of a few segments or each consisting of many segments; leaf segments bilobed or trilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate or elliptic, at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices caudate or acuminate; *ultimate segments* 12–20 cm long, free from penultimate segments or rarely confluent with penultimate segments; other segments 5–15 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions, or rarely confluent with the basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, with spiny projections (sometimes); tertiary veins obscure above and weakly raised below; *bracteoles* 3 or 4, 6–18 × 1.5–2 cm, dark brown to pink, the longest one ± as long as the peduncle or shorter than the peduncle, covering up to 1/3 of the spathe. *Inflorescence* solitary or rarely two, appearing before new leaf; *peduncle* 5–18 cm long above ground, 0.5–0.8 cm diam. at midpoint, often almost completely subterranean (less than 10 cm above ground level), scarcely mottled, gray or whitish green, with irregular very weak protuberances; *spathe* 6–12 cm long, 3–5 cm wide, cymbiform, cucullate, arching to 45°, apex acuminate; inner surface semiglossy, violet-purple, with translucent area obvious, 0.5–1 cm high, shorter than spadix; outer surface maroon, tinged green, matte; margins entire or sometimes wrinkled, scarcely to slightly overlapping at the base; veins obscure to conspicuous inside, conspicuously darker or paler than the spathe, purple; *spadix* exposed, stipitate, cylindric, narrower at apex, purple, 2.5–

Figure 21. A–D, *Dracontium polyphyllum*. —A. Inflorescence at anthesis in face view (*G. Zhu 1462*). —B. Infructescence with persistent spathe (*Croat 74210*). —C. Habit of plant with leaf and infructescence (*Croat 74284*). —D. Seeds in side view (*Croat 74210*).

4.2 cm long, 1–1.2 cm diam. at anthesis, never with appendages at apex; stipe 0.5–0.8 cm long, 0.4–0.8 cm diam. at anthesis, pale green or light brown. Flower tepals 4 to 5(to 6), 2–4 mm long, 1–2 mm wide, purple or light brown; stamens 5 or 6 to 7; filaments 2–3 mm long; anthers 1–2 mm long, slightly exserted; ovary 3-locular or 3- or 4-locular (rarely), pale green; stigma 2-lobed or often 3-lobed; style 0–2 mm long above tepals, purple, persistent. *Infructescence* with spadix 5–16 cm long, 3–4 cm diam. in fruit; *berries* 3-seeded, 0.5–0.7 cm diam., 1–1.5 cm thick, subglobose, 3- to 6-angular, apically subtruncate; young berries pale green; mature berries greenish purple; *seeds* 0.5–0.7 cm diam., reniform, light brown, laterally raised; dorsal ridges obvious, 1, continuous, with the central ridge contrastingly raised, more than 1 mm thick, 0.5–1 mm high, warty along both sides, appearing as strongly reduced lateral ridges. Chromosome number $2n = 26$ (*Croat 74210*).

Phenology. Flowering from December to June, with the peak probably from December to January; mature fruits are only collected in February.

Distribution and habitat. *Dracontium polyphyllum* ranges from the Atlantic coast of Surinam and French Guiana to northern Brazil (Pará State) and Amazonian Venezuela (Bolívar and Portuguesa States). It occurs in *Tropical moist forest* (T-mf) and *Premontane wet forest* (P-wf) life zones (Holdridge et al., 1971), at elevations of 0 to 220 m.

Local names. "Mai-eri" (*Balée 2106*, NY); "kao aj" (*Sauvain 175*, K).

Discussion. *Dracontium polyphyllum* is distinguished by its often subterranean peduncle, usually broadly opened spathe with a glossy inner surface, and smooth, laterally convex seeds. Historically, it has been confused with *D. asperum* (see discussion of *D. asperum*). It is also similar to *D. guianense*, which differs in having the above-ground portion of the peduncle much longer than the spathe. The shape of the spathe of *D. polyphyllum* is similar to that of *D. dubium*, but the inner surface of the spathe is semiglossy in the former and is covered with translucent scales in the latter.

Dracontium asperum K. Koch var. *wallisii* Engl. is synonymized here under *D. polyphyllum* for the first time. The name *Dracontium asperum* var. *wallisii* had been synonymized with *D. asperum* previously (Engler, 1911). However, *D. asperum* var. *wallisii* has a variegated blade, which shows that it belongs to *D. polyphyllum*.

Under the name *Echidnium spruceanum* Schott, Regel (1866: 98, t. 503) described a species based on a plant collected by Appun, presumably in Venezuela, with a plate. This species was later named as *E. regelianum* Engl. (1879: 286) in memory of E. Regel, citing the plate of the plant published by Regel (1866: t. 503). In the protologue of *E. regelianum*, Engler (1879: 287) only mentioned the collector's name "Appun" and did not designate a type. The plate (Regel, 1866: t. 503) was designated as a lectotype of *E. regelianum* by Bogner (1985: 78) when he made the combination *Dracontium regelianum* (Engl.) Bogner. No herbarium material related to the original description has been found. All characters from the description and the lectotype suggest it is conspecific with *D. polyphyllum*.

Wallis (1861) collected a plant he called "*Amorphophallus dubius* (*Dracontium polyphyllum*)" on an exploration trip to Pará in northern Brazil, and published a sketch of the plant in its natural habitat along with his field notes. Regel (footnote in Wallis, 1861: 332) suggested that the plant might be a new species and later published a color illustration of the same plant received from Wallis under the name *A. wallisii*, with a clear statement that the name was provisional and that it might end up being a "form" of an already described species (Regel, 1862). Thus, according to Article 34 of the current *International Code of Botanical Nomenclature* (Greuter et al., 2000), the name *A. wallisii* Regel is of no taxonomic value. Engler (1878) intended to use the name *A. wallisii* as the basionym of a new combination, *D. asperum* var. *wallisii*, but this name is no longer considered published, so actually Engler published a new name for his variety. Engler provided a description and cited one specimen he saw for this variety. Because Regel's name is not validly published, this specimen must be considered the type.

Additional specimens examined. BRAZIL. **Pará:** Lageira, airstrip on Rio Maicuru, *Strudwick et al. 3987* (MG, NY); Altamira, Igarapé Ipixuna, affluent of Rio Xingu, Araweté Indian Reserve, *Balée 2106* (MO, NY); Barcarena, Itupanema, São Caetano, km 12, *Gély 60* (MG); Conceição do Araguaia, ca. 20 km W of Redenção, near Côrrego São João & Troncamento Santa Teresa, *Plowman et al. 8616* (MG, MO, NY); Oriximiná, Campos do Ariramba, Serra da Preciosa, 20 km N of Ponte do Rio Cuminá-Mirim, *Martinelli et al. 6815* (MG, NY); Rio Xingu, Altamira, *Dias 513* (MG). FRENCH GUIANA. **Locality unknown:** *Leprieur s.n.* (P), *Richard s.n.* (P), *Broadway 407* (GH, NY, US); Chemin de la source de Baduel, *Jacquemin 2191, 2194* (CAY); Colline du Montabo, *Riera 415* (CAY); Montagne des Nouragues, Bassin de l'Approuague, Arataye, *Larpin 998* (CAY); village Boni de Locu, Bassin du Maroni, Lawa, *Fleury 802* (CAY, MO, P, U); Mont Cabassou, *Cremers & Crozier 14308* (CAY). **Acarouany:** *Sagot 608* (P); Bassin de l'Approuague, Crique Kapiri, *Cremers 11618* (CAY); Montagnes de Kaw, *Cremers 7682* (BR, CAY, K, P, US); S of Cayenne, along Route de Montagne Trésor, along side trail to Placer Trésor, *Feuillet 3993*

(CAY, K, NY, P, U, US); Montagne du Mahury, Sentier du Rorota, *Cowan 38843* (NY, P); Piste Sophie, La Gréve, *Hallé 790* (CAY, P, U, US); Route du Rorota, *Paris 36* (CAY); Petit Tukuchi, *Grenand 1913* (CAY); Saül N of Eaux Claires along rd. to Béllizon, *Croat 74210* (CAY, MO, K, US); Saül, Saint Laurent du Maroni, *Moretti 122* (CAY). **Saut Mapaou:** bassin de l'Approuague, *Cremers 12734* (CAY). SURINAM. Jodensavanne-Mapane creek area, *Bosbeheer 9845* (U); Sectie O, *Pulle 161* (U). **Brokopondo:** Banafokonde on Surinam River, *Sauvain 175* (BBS, CAY, K, P); Browns Berg Nature Reserve, *Kastelein 16153* (BBS). **Commewijne:** Akinto Soela, Mapanegebied, *Sang 16866* (BBS); Mapanegebied, *Elburg 9845* (BBS). **Paramaribo:** Rijsdijkeg, ca. 25 km S Paramaribo, *Lindeman 4608* (U); achter Cultuurtuin, *Stahel s.n.* (B). VENEZUELA. **Bolívar:** Río Caura, Caño La Ceiba (Caño Cumaca), *Stergios & Delgado 12940* (MO, PORT). **Portuguesa:** Est. Biol. Pozo Blanco, *Mori et al. 9666* (NY).

Cultivated plants. French Guiana. Cult. Paris Museum, France, *Mélinon s.n.* (P); collected by Joep Moonen in March 1993, received from J. Boos, cult. MBG, *G. Zhu 1440, 1441* (MO); Cayenne, cult. MBG [vouchered as *Croat 74210*], *G. Zhu 1462, 1513* (MO). Brazil. Espírito Santo, cult. MBG [vouchered as *Croat 71785*], *Zhu 1483, 1488* (MO); originally collected by H. van der Werff, cult. MBG [vouchered as *Croat 71785*] (MO). Singapore. Behind repair shed, *Nicolson 1119* (US).

19. Dracontium prancei G. Zhu & Croat, sp. nov. TYPE: Brazil. Amazonas: Pico Rondon, km 211, Perimetral Norte Hwy., 1°32′N, 62°48′W, 2 Feb. 1984, *G. Prance, I. L. do Amaral, J. Pipoly, A. Tavares, C. D. A. la Mota & A. Cress 28732* (holotype, NY!). Figure 22.

Petiolus 1.6–2.5 m longus; pedunculus subterraneanus, 1–5 cm longus; spatha (10)15–18 cm longa, 3.2–4 cm lata; extus purpurea; intus velutina, purpurea; spadix (2.5)4–5 cm longus, 0.9–1.2 cm diam.; tepala 5; baccae globosae, 1–1.2 cm diam.; semina brunneola vel fusca, 0.5–0.6 cm diam.

Tuber hemispherical, 8–14 cm diam., 6–9 cm thick, flat above, rounded and white to brown below, 10–15 cm below ground level; tubercles abundant, rounded, 0.5–1 cm diam., borne around the periphery of tuber; roots whitish, to 0.3 mm diam.; *cataphylls* 4 or 5, 4–20 cm long, 2.5–4 cm wide, pink to light brown, 5–15 cm long above ground. *Leaves* solitary or sometimes two or more per tuber; *petioles* 1.6–2.5 m long above ground, 2.5–3.5 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blade* spreading horizontally, 1–1.2 m diam., papyraceous, sometimes fenestrate, never variegated, without raphide cells or dark markings, glossy and medium green above, semiglossy and medium green below; *middle division* twice trichotomously branched, 55–65 × 50–60 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions once or twice dichotomously branched, 50–60 × 55–60 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free from each other, each consisting of many segments; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments; apices acuminate; *ultimate segments* 10–13 cm long, free from penultimate segments; other segments 3–12 cm long; penultimate segments free from the subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins conspicuous above and weakly raised below; *bracteoles* 3 or 4, 7–14 cm long, 3–5 cm wide, pink and light brown, the longest one longer than the peduncle, slightly covering the base of the spathe. *Inflorescence* solitary or sometimes two, appearing before new leaf; *peduncle* 1–5 cm long above ground, 1–1.2 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, brownish green or whitish tinged pink, smooth; *spathe* (10–)15–18 cm long, 3.2–4 cm wide, cymbiform, cucullate, arching up to 45°, apex acuminate; inner surface semiglossy or velvety, maroon or blackish purple, with translucent area obvious, 0.5–1 cm high, shorter than spadix; outer surface maroon (sometimes tinged green), matte; margins entire, broadly overlapping in the lower two-thirds; veins obscure inside and raised outside, conspicuously darker or paler than the spathe; *spadix* hidden, stipitate, cylindric, narrower at apex, purple or brownish purple, (2.5–)4–5 × 0.9–1.2 cm at anthesis, never with appendages at apex; stipe 0.5–0.8 cm long, 0.5–0.7 cm diam. at anthesis, purple. Flower tepals 5, 1.5–2.5 mm long, 1–2 mm wide, purple or brownish purple; stamens 6 or 7; filaments 1–2.5 mm long; anthers 0.5 mm long, completely exserted; ovary 3-locular, pale green; stigma 3-lobed; style 1–2 mm long above tepals, purple, persistent. *Infructescence* with spadix 5.5 cm long, 2.4 cm diam. in fruit; *berries* 1-seeded, 1–1.2 cm diam., 0.8–1 cm thick, subglobose, 3- to 6-angular, apically truncate; young berries light green; mature berries color unknown, with abundant raphide cells; *seeds* 0.5–0.6 cm diam., reniform, light brown or dark brown, laterally flattened; sparsely beset with irregular warts dorsally, dorsal ridges obscure. Chromosome number $2n = 26$ (*Croat 73867*).

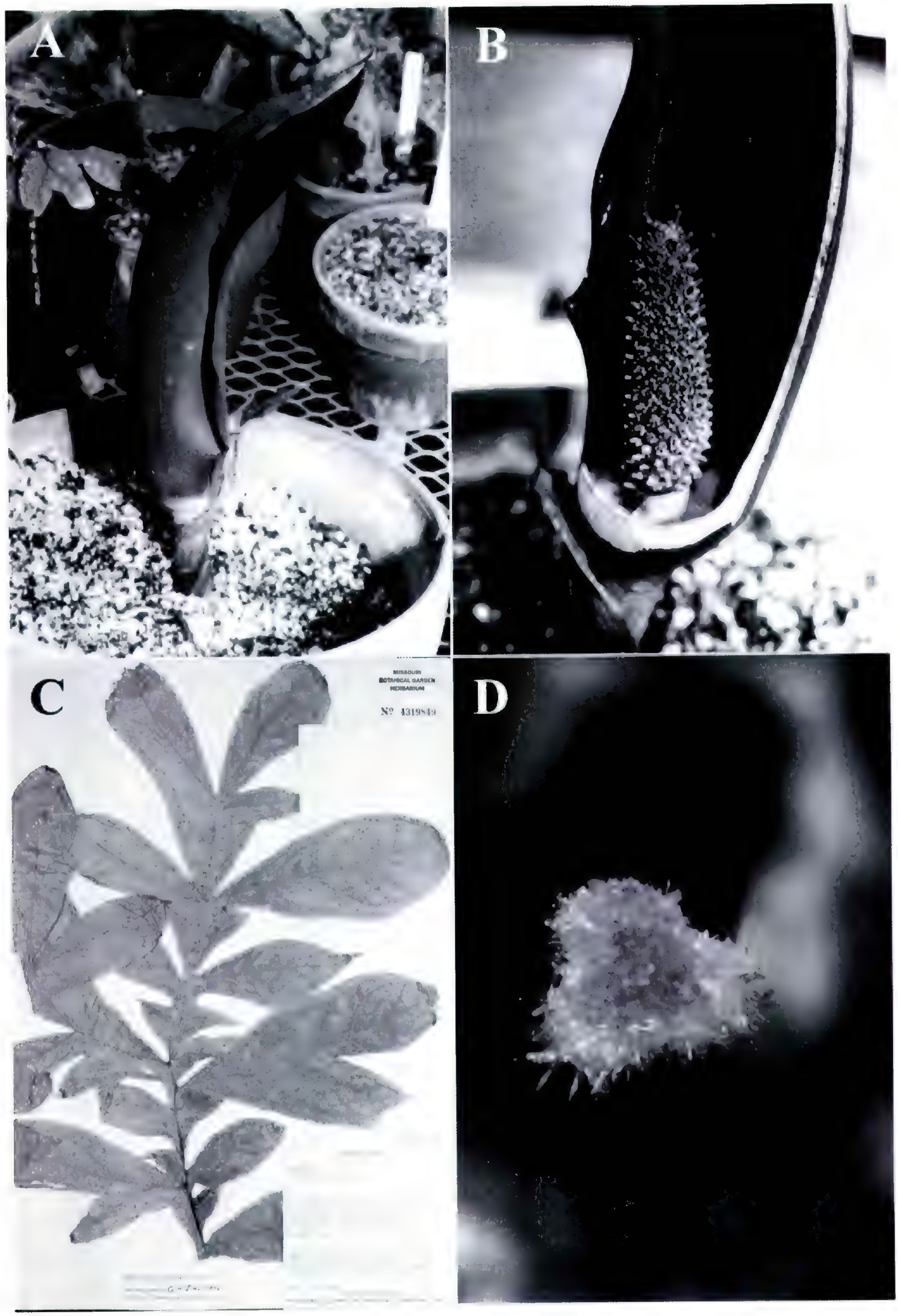

Figure 22. A–D, *Dracontium prancei*. —A. Inflorescence in side view (*Croat 73867*). —B. Inflorescence with spathe cut away to expose spadix. —C. Apical portion of leaf blade (*G. Zhu 1455*). —D. Close-up of stigma (*G. Zhu 150*).

Phenology. Flowering known only in February; mature fruits are known only in May.

Distribution and habitat. *Dracontium prancei* is known only from Brazil in the states of Amazonas and Roraima. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at elevations of 50 to 150 m.

Discussion. *Dracontium prancei* may be confused with *D. asperum* because of the similar sizes and shapes of the spathe, but the latter species differs in having bracteoles much shorter than the peduncles and never reaching the spathe (in contrast to elongate bracteoles that subtend the entire peduncle, even over the base of the spathe in *D. prancei*). *Dracontium prancei* has a short peduncle up to 5 cm above ground while *D. asperum* has a peduncle 5 to 17 cm above ground. Live plants of this species of unknown origin were widely distributed by the Munich Botanical Garden under the name *D. polyphyllum*, which differs from *D. prancei* in having a much shorter spathe 6–12 cm long versus (10–)15–18 cm long in *D. prancei*. The spadix is usually exposed in *D. polyphyllum* and completely embraced by the spathe in *D. prancei*. *Dracontium prancei* is another species that is easily grown and has great horticultural value. It grows rapidly, propagates easily by tubercles, and blooms regularly in cultivation. A plant of *D. prancei* is cultivated in the Climatron® at the Missouri Botanical Garden.

Dracontium prancei is named in honor of Ghillean Prance, whose many collections throughout the Amazon basin of Brazil include the type specimen of this species.

Paratype. BRAZIL. **Roraima:** SEMA Ecol. Res., S of Cachoeira de FumaHa, 24 July 1987, *Milliken et al. 511* (K).

Cultivated plants. Origin unknown. Collected by J. Bogner, cult. at Munich Botanical Garden, Germany, 28 May 1994, *J. Bogner 1132* (M), *G. Zhu 1501* (MO). Originally from Munich Botanical Garden, Germany, received from W. Hetterscheid in Holland, cult. MBG, *T. B. Croat 73867* (MO), *G. Zhu 1458, 1463* (MO).

20. Dracontium purdieanum (Schott) Engl., Pflanzenr. IV. 23C (Heft 48): 45. 1911. *Ophione purdieana* Schott, Oesterr. Bot. Wochenbl. 7: 101. 1857. TYPE: Colombia. Magdalena: Santa Marta, 1845, *W. Purdie s.n.* (holotype, K!). Figure 23.

Dracontium aricuaisanum G. S. Bunting, Phytologia 60: 301–302. 1985. TYPE: Venezuela. Zulia: Dtto. Perijá, outskirts of Est. Hidrol. Aricuaisá-Pie de Monte, 9°35′30″N, 72°53′55″W, 100–250 m, 25 Feb.–3 Mar. 1982, *G. S. Bunting, G. Panapera & H. Lobo 10866* (holotype, NY!; isotype, VEN!).

Tuber hemispherical, 4–6 cm diam., 3.5–4 cm thick, flat above, rounded and white to brown below, 9–16 cm below ground level; tubercles abundant, obovoid, 0.5–0.9 cm diam., 1–1.5 cm long, borne around the periphery of tuber; roots white, to 3 mm diam.; *cataphylls* 3 to 4, (3–)9–17 cm long, 2–3 cm wide, whitish to light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–1.8 m above ground, 2.5–4 cm diam. at midpoint, dark green or brownish green (tinged gray), contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, smooth; juvenile blade sagittate, or sagittately lobed; mature *blade* spreading horizontally, 0.8–1.2 m diam., papyraceous, sometimes fenestrate, sometimes variegated, with abundant raphide cells and dark markings (1–2 mm long), semiglossy and medium green above, glossy and dark green below; *middle division* twice trichotomously branched, 50–65 × 40–55 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 50–60 × 45–50 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each usually consisting of a single segment; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments; apices acuminate, or acute, or caudate (sometimes); *ultimate segments* 9–20 cm long, free from penultimate segments; other segments 1.5–10 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins obscure above and weakly raised below; *bracteoles* 3 to 4, 9–25 cm long, 2–3 cm wide, light brown, the longest one ± as long as the peduncle, reaching the spathe. *Inflorescence* solitary, appearing before new leaf; *peduncle* 0–5 cm long above ground, 0.8–1 cm diam. at midpoint, often almost completely subterranean (0–5 cm above ground level), scarcely mottled, brownish green, with irregular protuberances or spiny projections (sometimes); *spathe* 6–15 × 1.8–3.5 cm, non-cymbiform, broadened at a certain point and differentiated into a proximal tube and a distal lamina (blade), non-cucullate, arching to 45°, apex acuminate; 1.5–3 × 1.8–3.5 cm at widest point; lamina 2 to 3 times longer than the tube; inner surface covered with dense, translucent scales 1–2 mm long, violet-purple or olive-brown, with translucent area obscure; outer surface violet-purple, tinged green, matte; margins entire, broadly

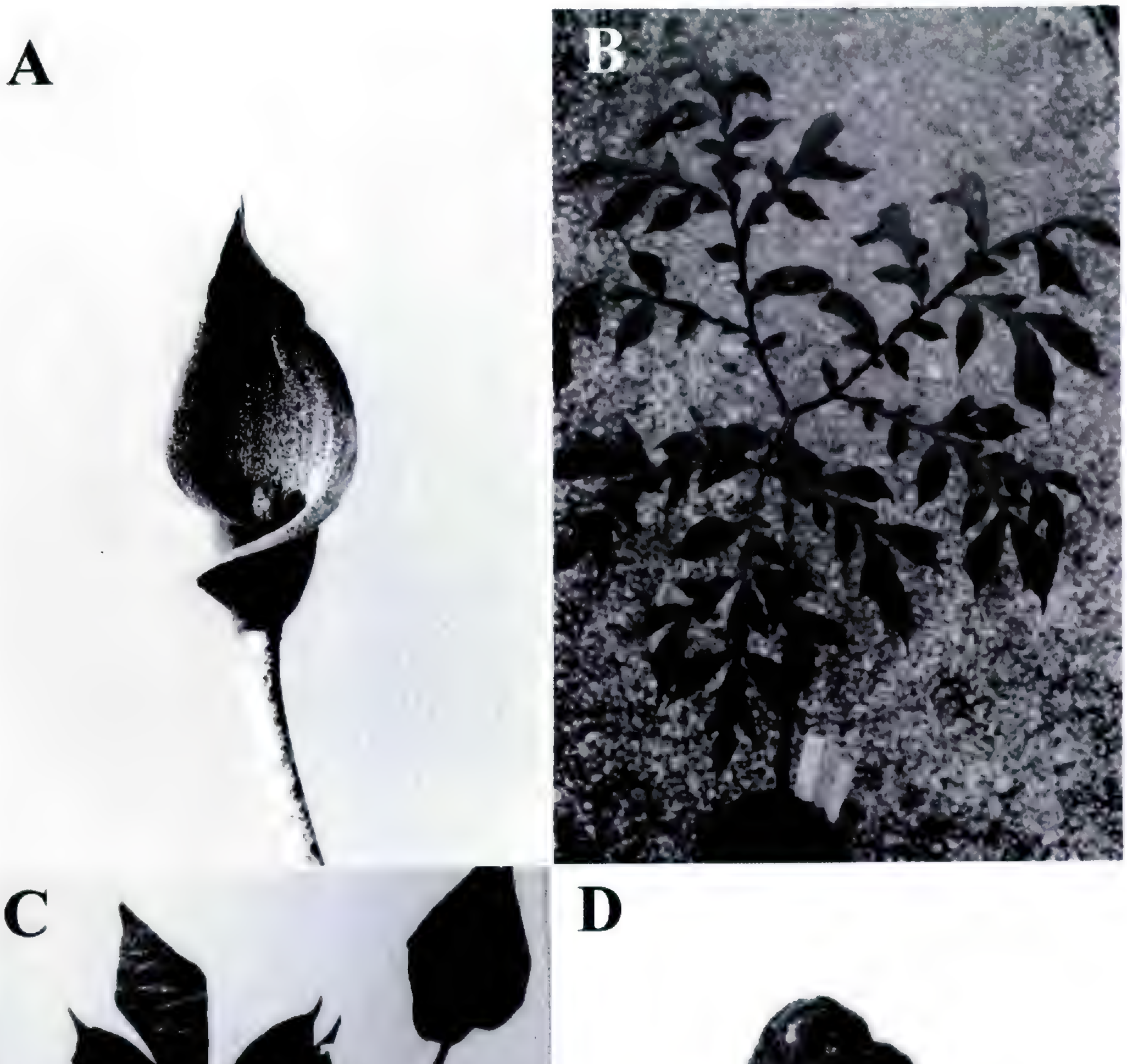

Figure 23. A–D, *Dracontium purdieanum*. A, B, (*Aristeguieta s.n.*). —A. Inflorescence at anthesis. Photo by J. Bogner. —B. Cultivated plant with leaf at Munich Botanical Garden. —C. Type specimen of *D. aricuaisanum* G. S. Bunting. —D. Seeds in lateral view (*Bunting 11463*).

overlapping at the base; veins conspicuous inside, conspicuously darker or paler than the spathe, purple; *spadix* exposed, sessile or stipitate, cylindric, brownish purple, 2–4 cm long, 0.5–1 cm diam. at anthesis, often with one to a few appendages at apex, 0.2–0.5 cm long when present; stipe 0.8 cm long, 0.5 cm diam. at anthesis, light brown. Flower tepals 4 to 6(to 7), 1–2 mm long, 1 mm wide, green or light brown; stamens 6 or 7; filaments 1–2 mm long; anthers 0.5 mm long, slightly exserted; ovary 3- to 5-locular, pale green; stigma 3- or 4-lobed; style 0.5–1 mm long above tepals, greenish, not persistent. *Infructescence* with spadix 4.5–5 cm long, 3.5–4 cm diam. in fruit; *berries* (1)3- to 4(5)-seeded, 1–1.2 cm diam., 1–1.3 cm thick, subglobose, 3- to 6-angular, apically truncate; young berries dark green; mature berries purplish red, sometimes with abundant raphide cells; *seeds* 0.5–0.7 cm diam., reniform, dark brown, laterally depressed; dorsal ridges obvious, 3 continuous ridges (sometimes with 1–2 strongly intermediate interrupted dorsal ridges), less than 0.5 mm thick, 0.3 mm high, warty along ridges. Chromosome number $2n = 26$ (*Aristeguieta s.n.*; Petersen, 1989).

Phenology. Flowering from February to March; mature fruits from April to May.

Distribution and habitat. *Dracontium purdieanum* is known only from the Caribbean coastal departments of Atlántico, Magdalena, and Bolívar in Colombia, and Zulia, Venezuela. It occurs in *Tropical moist forest* (T-mf) and *Premontane moist forest* (P-mf) life zones (Holdridge et al., 1971) along the coast, at elevations from sea level to 250 m.

Discussion. *Dracontium purdieanum* is characterized by having the inner surface of the spathe densely covered with translucent scales (1–2 mm long), and a spadix that often has appendages at the apex. This species is vegetatively similar to *D. dubium* but differs from that species in having seeds with 3 continuous ridges (sometimes with 1–2 strongly intermediate interrupted dorsal ridges).

In 1845, a year after Schomburgk's expedition to British Guiana (Guyana), William Purdie collected a second plant presently included in *Dracontium* from the vicinity of Santa Marta, Magdalena Department, Colombia. This collection was named *Ophione purdieana* Schott as a new unispecific genus, which differs from *Dracontium* in having a long-acuminate spathe (Schott, 1857a). Later, Engler (1911) placed this species in *Dracontium*, citing "*D. purdieanum* (Schott) Hook. f. in Bot. Mag. (1873) in observatione ad tabulam 6048." However, no such combination was made by J. D. Hooker in that publication. Instead, Engler himself validly published the combination (1911: 45), citing the basionym after *D. purdieanum*, which combination must therefore be attributed to "(Schott) Engler" according to the *Code* (Art. 46, Greuter et al., 2000).

In the protologue of *Ophione purdieana* Schott (1857a: 101), there is no explicit type designation, but it was clearly stated that the name, which honors the collector, was based on a gathering made by "Purdie" from "St. Marta." This constitutes mention of a single gathering as indication of the type (Art. 37.3, Greuter et al., 2000). A specimen (*Purdie s.n.*, K, 1845) collected near Santa Marta in Colombia is evidently the same one used by Schott when describing *O. purdieana*. Schott (1858b: t. 89) published an illustration of the species a year after its original description. The spathe in the illustration matches that of *Purdie s.n.* in great detail. *Purdie s.n.* can therefore be regarded as the holotype of *O. purdieana* Schott.

More than a century after its discovery, *Dracontium purdieanum* was re-collected and redescribed by Bunting (1986) as *D. aricuaisanum* from Aricuaisá–Pie de Monte in Zulia State, Venezuela. Bunting's new species differed from *D. purdieanum* in no significant way.

Additional specimens examined. COLOMBIA. **Atlántico:** along trail from Luruaco to Piñar de Candelaria, *Dugand 1161* (F). **Bolívar:** lands of Loba, Caño Papayal, vic. of Estrella, *Curran 349* (GH, US). VENEZUELA. **Zulia:** betw. Aricuaisá [Ariguaisá] & Pie de Monte on Río Aricuaisá, 55 km SW of Machiques by air, *Liesner & González 13060* (MO, VEN).

Cultivated plants. Venezuela. Zulia, Aricuaisá, cult. at Munich Botanical Garden, Germany, *Aristeguieta s.n.* (M).

21. Dracontium soconuscum Matuda, Amer. Midl. Naturalist 41: 494. 1949. TYPE: Mexico. Chiapas: Soconusco, Santa Elena, 16 km W of Acapetagua, 30 m, Jan. 1947, *E. Matuda 17780* (lectotype, designated here, MEXU 85137! pro parte, inflorescence; isotypes, MEXU!, NY!). Figure 24.

Dracontium dressleri Croat, Selbyana 1: 168. 1975. Syn. nov. TYPE: Panama. Canal Zone: Barro Colorado Island, near end of Zetek trail, 30 June 1972, *R. Dressler s.n.* (holotype, MO!).

Tuber hemispherical or rounded, 4–7 cm diam., 5–9 cm thick, flat above, rounded and white to brown below, 4–45 cm below ground level; tubercles few, cylindrically elongated, 0.5–0.8 cm diam., 0.5–1 cm long, borne around the periphery of tuber; roots whitish or sometimes tinged green, to 3 mm diam.; *cataphylls* 3 or 4, 3–47 cm long, 2–3.5 cm wide, pink or light brown (when dried), reaching

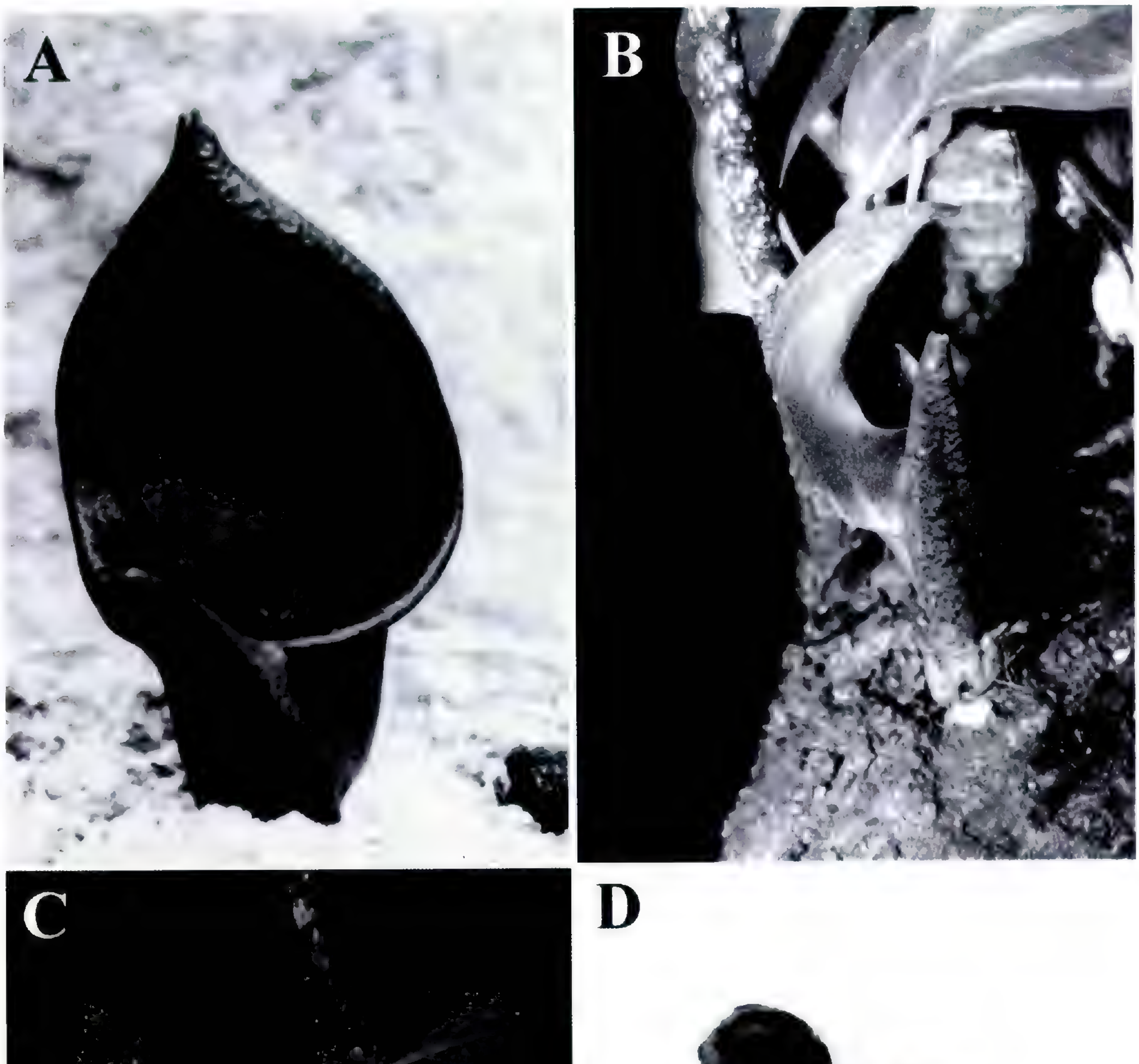

Figure 24. A–D, *Dracontium soconuscum*. —A. Cultivated by J. Bogner. Inflorescence at anthesis in face view. Photo by Bogner. B, C, (*G. Zhu 1502*). —B. Inflorescence side view. —C. Leaf blade adaxial surface. —D. Seeds in lateral view (*Bartlett & Lasser 16831*).

or surpassing ground level. *Leaves* solitary or sometimes two or more per tuber; *petioles* 1–1.8 m long above ground, 3–5 cm diam. at midpoint, dark green or gray or whitish green, sometimes tinged brown or red-brown, weakly mottled, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blade* ascending to 45° to the petiole spreading horizontally, 1–1.2 m diam., subcoriaceous papyraceous, sometimes fenestrate, never variegated, without raphide cells or dark markings, semiglossy and dark green above, matte and medium green below; *middle division* 3 times or more trichotomously branched, 0.8–1.5 × 0.6–1 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions 3 times or more dichotomously branched, 0.8–1 × 0.5–0.8 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free, each consisting of many segments; leaf segments bilobed, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate or orbicular-ovate, at least some of the basal segments free from each other, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate, or acute; *ultimate segments* 7–17 cm long, free from penultimate segments or rarely confluent with penultimate segments; other segments 5–15 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments absent, free from each other; rachises patterned similar to petiole but in much paler shades, similar to petiole but in a much paler scale; tertiary veins obscure above and weakly raised below; *bracteoles* 1 to 3, 5–45 cm long, 1.5–2.5 cm wide, pink to light brown, the longest one longer than the peduncle, covering the basal half or more of the spathe. *Inflorescence* solitary or rarely two, appearing before new leaf; *peduncle* 4–45 cm long above ground, 0.8–1.2 cm diam. at midpoint, often almost completely subterranean (0–5 cm above ground level), scarcely mottled, whitish tinged pink, smooth; *spathe* 6–8(10) cm long, 3–4(6) cm wide, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucullate, arching 45°–90°, apex acuminate; 1–3 cm long, 2.5–4(5) cm wide at widest point; lamina similar to the tube in length (or slightly longer); inner surface glossy, violet-purple or maroon, with translucent area obscure; outer surface olive-brown or maroon, semiglossy; margins entire, broadly overlapping in the lower half; veins obscure inside or raised outside, similar to the spathe in color, purple; spadix exposed, stipitate, cylindric, violet-purple, 1–4 × 0.5–1 cm at anthesis, often with several appendages at apex, 0.5–0.8 cm long when present; stipe 0.3–0.7 × 0.5–0.6 cm at anthesis, light brown. Flower tepals (4)5 or 6(8), 2–2.5 mm long, 1 mm wide, dark purple; stamens (5)6 or 7(9); filaments 1–1.5 mm long; anthers 1–2 mm long, slightly exserted; ovary 2- to 5-locular, pale green; stigma 3-lobed; style 0–1 mm long above tepals, dark purple, not persistent. *Infructescence* with spadix 4–10 cm long, 2–3.5 cm diam. in fruit; *berries* 4-seeded, 0.8–1.4 cm diam., 1–1.5 cm thick, subglobose, 4- to 5-angular, apically truncate; young berries dark green; mature berries purplish brown, with abundant reddish dots; *seeds* 0.6–0.9 cm long, 0.5–0.6 cm diam. (wide), reniform or triangular (±), dark brown, laterally depressed; dorsal ridges obvious, 3, continuous, monomorphic, more than 1 mm thick, 0.1–0.5 mm high, warty along both sides, appearing as strongly reduced lateral ridges.

Phenology. Flowering from October to April; mature fruits from April to August.

Distribution and habitat. The northernmost species of the genus, *Dracontium soconuscum* is known from the Pacific slope in southern Mexico (Chiapas) and northern Costa Rica (Guanacaste, Alajuela, Puntarenas), and on the Caribbean slope in central Panama (Canal Zone). It occurs in costal lowland thicket or bushes of the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), from sea level to about 1100 m.

Local names. "Cola de tigre" (*E. Matuda 17780*, MEXU, NY).

Discussion. *Dracontium soconuscum* is easily confused vegetatively with *D. grayumianum*, but that species differs in having seeds with five or six strongly interrupted dorsal ridges, whereas *D. soconuscum* has seeds with three obvious and continuous dorsal ridges.

According to the protologue, the type of *Dracontium soconuscum*, *E. Matuda 17780*, consists of a holotype in the Matuda Herbarium (CHIS) and two isotypes (MEXU 6739, F). The holotype was later transferred to MEXU (MEXU 85137) and the isotype intended for F was evidently sent to NY instead. The type is a mixed collection of two gatherings prepared by the same collector in January and May, 1947, respectively. Since a type can only be a single gathering (Art. 8, Greuter et al., 2000), the inflorescence on MEXU 85137 is designated here as the lectotype of *D. soconuscum*.

There are three other gatherings existing under

the same collection number: *Matuda 17780* (MEXU 47893) collected from Cruz do Piedra, January and May 1947; *Matuda 17780* (MEXU 85107) collected from Nandolopez, January and May 1947; and *Matuda 17780* (MEXU 141842) collected from Santa Teresa, Acapetagua, on 14 July 1947.

Additional specimens examined. COSTA RICA. **Alajuela:** Finca Carlos Gómez, Orotina, *Chacón 1414* (MO); La Balsa de Río Grande, *Pittier 3650* (US). **Guanacaste:** Río Higuerón, near Taboga, *Liesner et al. 2720* (MO). **Puntarenas:** rd. to Monteverde, *Luteyn 3394* (DUKE); Garabito Canton, Res. Biol. Carara, along S side of Río Grande de Tárcoles, from Carretera Constanera to Río Carara, *Grayum et al. 11108* (MO). MEXICO. **Chiapas:** Mazapa, 10 km E of Motozintla, *Garcia et al. 1527* (BM). PANAMA. **Canal Zone:** *Pittier 3429* (US); Barro Colorado Island, Zetek Trail, *Croat 27795* (MO); Juan Mina, Chagres River, *Bartlett & Lasser 16831* (F, MO, NY); vic. Summit Hills Golf Course, *Croat 27794* (MO). **Coclé:** Camp Piña, *Allen 3427* (MO). **Colón:** Achiote, 1974, *Dressler s.n.* (DUKE, PMA); Gamboa Country Club Marina, *Garwood 1639A* (F). **Panamá:** Río Agua Clara, Icantí, *Gentry 2598* (MO).

Cultivated plants. Panama. Barro Colorado Island, cult. Munich Botanical Garden [vouchered as *Croat 27795*], *Bogner s.n.* (M); Colón, Achiote, STRI [vouchered as *Dressler s.n.*], *G. Zhu 1502* (MO); Canal Area, cult. Fairchild Tropical Garden, Miami, Florida, U.S.A., *Fantz 4115, 4249* (FTG); cult. Selby Gardens, *Madison 3764* (SEL); cult. by Dewey Fisk, Florida (received from J. Boos), *G. Zhu 1485* (MO).

22. Dracontium spruceanum (Schott) G. Zhu, Novon 6: 308. 1996. *Echidnium spruceanum* Schott, Oesterr. Bot. Z. 8: 350. 1858. *Cyrtosperma spruceanum* (Schott) Engl., Martius, Fl. Bras. 3(2): 118. 1878. TYPE: Brazil. Amazonas: São Gabriel, May 1852, *R. Spruce 2406* (holotype, K!). Figures 3C, 3D, 25, 26.

Dracontium carderi Hook. f., Bot. Mag. t. 6523. 1880. Syn. nov. TYPE: Colombia. Apr. 1879, *N. E. Brown s.n.* (holotype, K! [3]). [Cultivated plant by Mr. Bull, originally collected by Carder in Colombia, locality unknown.]

Dracontium costaricense Engl., Pflanzenr. 4, Fam. 23C(44). 1911. Syn. nov. TYPE: Costa Rica. Limón: Talamanca, forest of Shirones, 100 m, Feb. 1895, *H. Pittier 9232* (holotype, BR!; isotype, B!).

Dracontium trianae Engl., Pflanzenr. 4, Fam. 23C(44). 1911. Syn. nov. TYPE: Colombia. Meta: Villavicencio, 400 m, Jan. 1856, *J. J. Triana 691* (lectotype, designated by Zhu (1996: 309), BM!; isotype, COL!).

Dracontium loretense K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 617. 1932. Syn. nov. TYPE: Peru. Loreto: lower Río Huallaga, 155–210 m, Oct.–Nov. 1929, *L. Williams 5144* (holotype, F!; isotype, US!).

Dracontium ornatum K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 15: 40. 1940. Syn. nov. TYPE: Ecuador. Pastaza: above Mera, 1100 m, 16 Nov. 1938, *A. Schultze-Rhonhof 2998* (holotype, B! [on sheet with *Schultze-Rhonhof 3031*]).

Tuber hemispherical, 4–18 cm diam., 3–10 cm thick, flat or slightly convex above, rounded and white to brown below, 15–40 cm below ground level; tubercles abundant, rounded, 0.5–2 cm diam., borne around the periphery of tuber; roots to 4 mm diam.; *cataphylls* 1 to 3, 10–40 cm long, 2–4 cm wide, pink to light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–3 m long above ground, 1.2–4 cm diam. at midpoint, dark green, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blade* spreading horizontally, 0.9–1.5 m diam., subcoriaceous to thinly coriaceous, rarely fenestrate, never variegated, without raphide cells or dark markings (often), semiglossy and dark green above, matte and medium green below; *middle division* once or twice trichotomously branched, 47–60 × 45–55 cm, with terminal subdivision never divided into sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 45–62 × 50–60 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections often free, each consisting of many segments; broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate or elliptic, mostly free from each other in each division, without contrastingly smaller rounded or triangular segments (often); apices caudate; *ultimate segments* 12–35 cm long, confluent with penultimate segments or free from penultimate segments; other segments 4.5–30 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned similar to petiole but in much paler shades, smooth; tertiary veins obscure above and weakly raised below; *bracteoles* 1 to 3, 4–45 cm long, 1–3 cm wide, pinkish or light brown, the longest one much shorter than the peduncle, confined at the base. *Inflorescence* solitary, appearing before or after new leaf; *peduncle* 60–150 cm long above ground, 2–3.5 cm diam. at midpoint, more than half as long as the petiole or sometimes as long as or longer than the petiole, mottled similar to petiole but deeper in color, dark green or brownish green, smooth or with irregular protuberances in lower half; *spathe* (20–)25–35 cm long, 3–6 cm wide, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade) or cymbiform (rarely), non-cucullate, erect or slightly arching, apex acuminate; 5–10 cm long, 3–6 cm wide at widest point; lamina 3 to 5

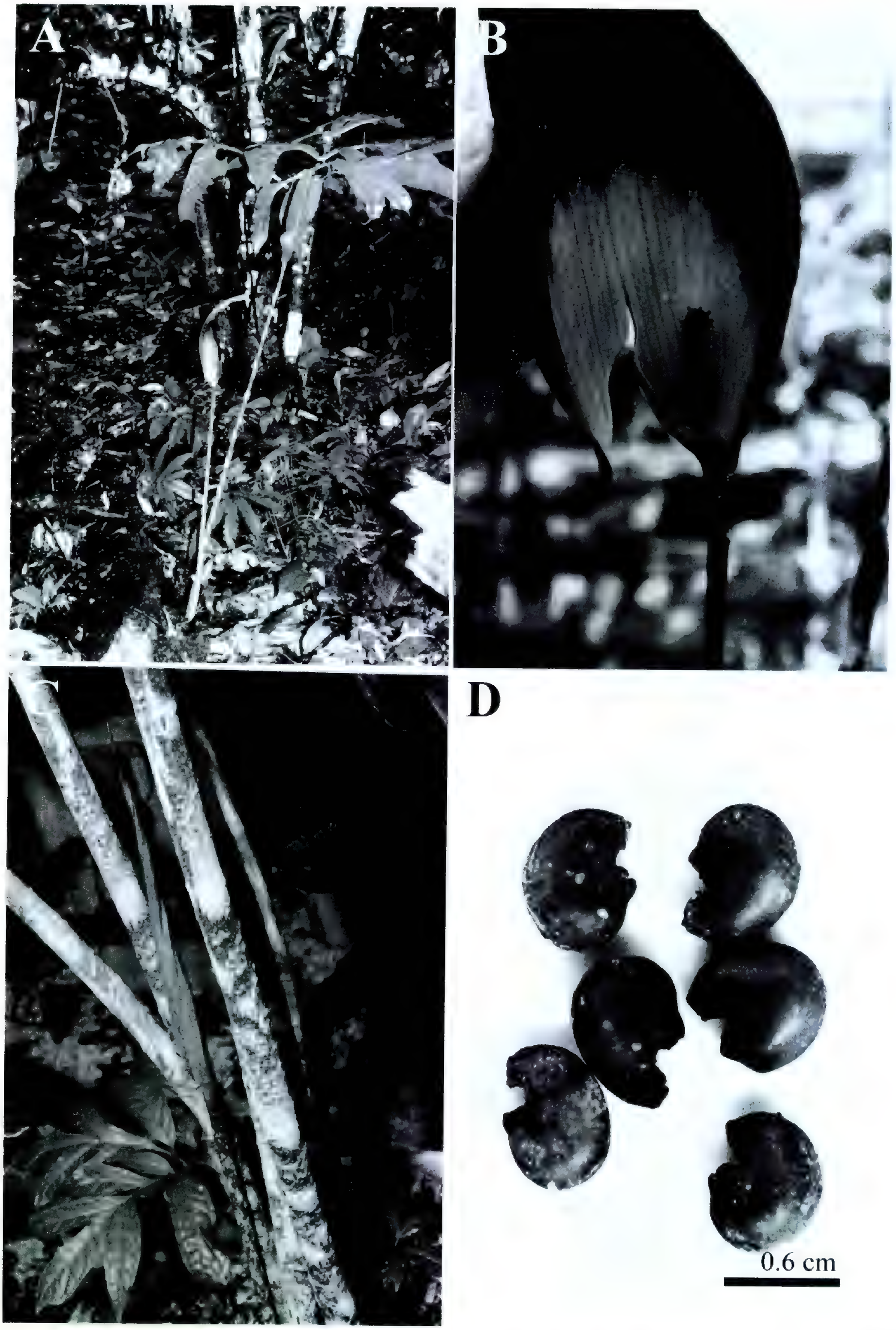

Figure 25. A–D, *Dracontium spruceanum*. —A. Habit showing flowering plant (*G. Zhu 1503*). —B. Spathe at anthesis split open to show the pale basal portion and the spadix (*G. Zhu 1486*). —C. Cultivated by Luis Bueno, Miami. Petioles and juvenile infloresence. —D. Seeds in lateral view (*Cerón 72368*).

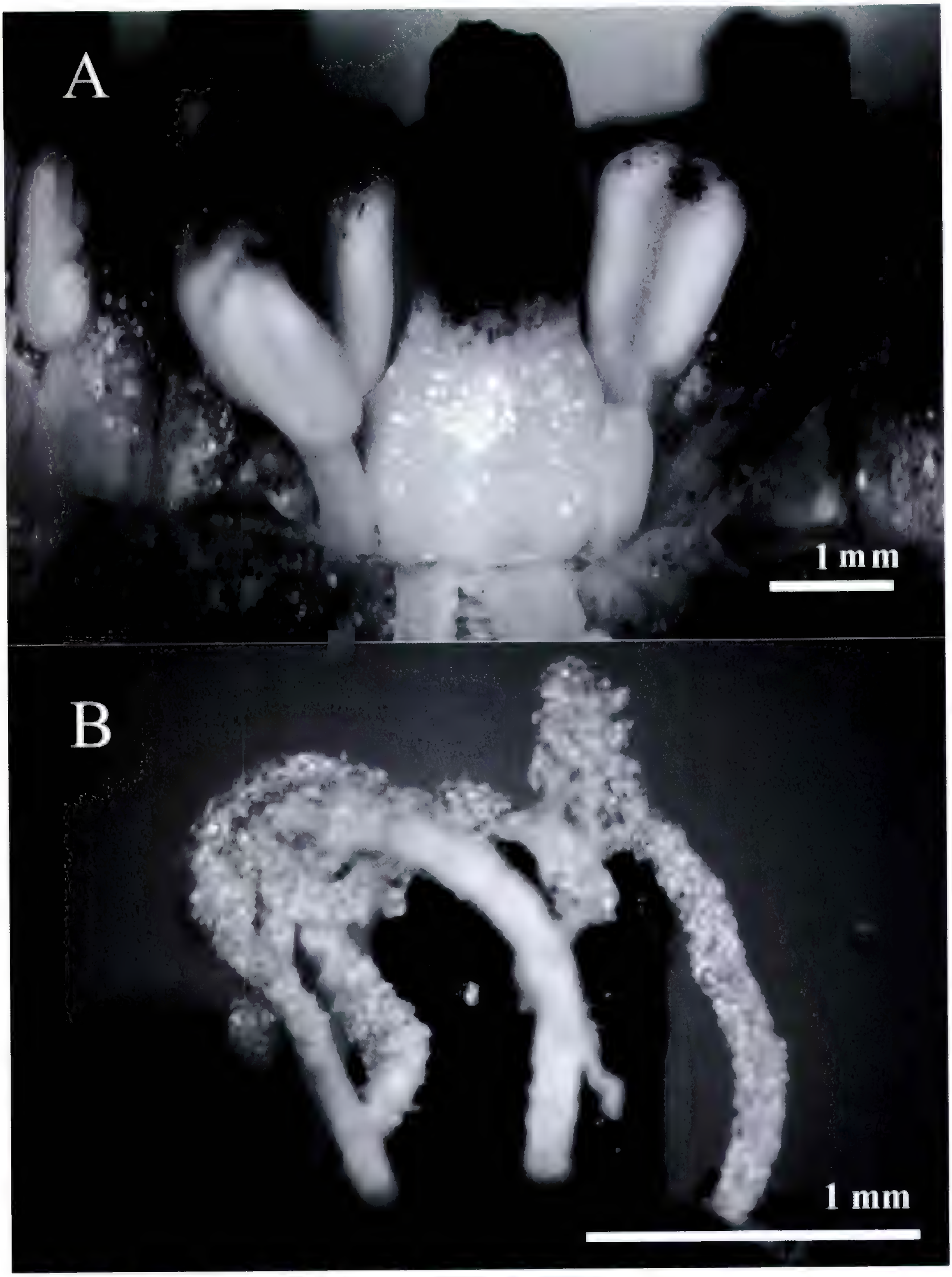

Figure 26. A, B, *Dracontium spruceanum* (*G. Zhu 1486*). —A. Side view of pistil showing unopened anthers. —B. Apex of flower showing tip of pistil with emerging threads of pollen.

times longer than the tube; inner surface semiglossy, maroon or olive-brown, with translucent area obvious, 4–8 cm high, 1.5 to 3 times longer than spadix; outer surface maroon, tinged green, or green, matte; margins entire, broadly overlapping at the base; veins obscure inside or raised outside, similar to the spathe in color; *spadix* hidden, stipitate, cylindric, purple or brownish purple or brown, (2.5–)3–4(–6.5) × 0.6–1 cm at anthesis, never with appendages at apex; stipe 0.5–0.8 × 0.4–0.6 cm at anthesis, pale green or light brown. Flower tepals 4 to 5, 1.5–2 mm long, 1–2 mm wide, purple; stamens 6 to 11; filaments 1–1.5 mm long; anthers 0.5 mm long, slightly exserted; ovary 3-locular, pale green; stigma unlobed, or 2- to 3-lobed; style 0.5–1 mm long above tepals, purple, persistent. *Infructescence* with spadix 8–16 × 2.5–3.5 cm in fruit; *berries* 1- or 2-seeded, 0.5–0.7 cm diam., 0.7–1 cm thick, globose or obliquely obovoid, apically rounded (sometimes slightly concave around the persistent style); young berries medium green; mature berries orange, without reddish dots and raphide cells; *seeds* 0.5–0.7 cm long, 0.4–0.5 cm diam., elongated or rounded, reddish brown, laterally depressed; dorsal ridges obvious, more than 3, strongly interrupted (often), with the central ridge contrastingly raised, more than 1 mm thick, 0.1–0.3 mm high, warty along ridges.

Phenology. Flowering throughout the year; mature fruits throughout the year.

Distribution and habitat. *Dracontium spruceanum* ranges from the Caribbean coastal plain of Costa Rica (Limón) to Colombia and Ecuador (on both sides of the Andes) and Amazonian Ecuador, Peru, Venezuela, and Brazil. It has also been collected from Surinam. It occurs in *Tropical moist forest* (T-mf), *Premontane wet forest* (P-wf), and *Tropical wet forest* (T-wf) life zones (Holdridge et al., 1971), at elevations of 25 to 1215 m.

Local names. "Tamá kida bari" (*La Rotta 586*, COL); "chupadera" (*Archer 1729*, US); "papayuëla" (*Idrobo & Cuatrecasas 2685*, COL); "machaqui mandi" (*Alarcon 62*, QCA); "jergón sacha" (*Vásquez & Jaramillo 4938*, MO).

Discussion. *Dracontium spruceanum* is the most morphologically plastic and widely distributed species in the genus. It is characterized by its usually erect or slightly arching (non-cymbiform) spathe, which differentiates into a proximal tube and distal lamina (blade), with the translucent area of the inner spathe surface 1.5 to 3 times longer than the spadix, and by having the rachises of the leaf blades usually naked.

Dracontium carderi, *D. costaricense*, *D. loretense*, *D. ornatum*, and *D. trianae* are synonymized here for the first time. The differences among the type specimens are slight. They closely resemble each other and the type of *D. spruceanum*, especially in spathe shape and peduncle length.

Dracontium spruceanum was first described by Schott (1858b) as *Echidnium spruceanum* in honor of Richard Spruce, who collected the holotype (*Spruce 2406*, K) at São Gabriel along the Rio Negro in Amazonas, Brazil. This name was later transferred to the genus *Cyrtosperma* by Engler (1878), and subsequently not considered to be a *Dracontium* based on Engler's inference of a unilocular ovary. This is a misinterpretation, since anatomical study indicates that the specimen is too young to yield accurate information (Richard Keating, pers. comm.). Further, specimens collected near the type locality usually have a single ovule in each of two or three locules per ovary.

Dracontium spruceanum shares a long peduncle with *D. asperispathum*, *D. croatii*, *D. grandispathum*, *D. longipes*, *D. peruvianum*, *D. pittieri*, and *D. plowmanii*. *Dracontium croatii*, *D. pittieri*, and *D. peruvianum* differ in having a cymbiform spathe that is not differentiated into a proximal tube and a distal lamina, whereas the others listed above have a non-cymbiform spathe that is constricted at the base to form a proximal tube and distal lamina. *Dracontium plowmanii* differs from *D. spruceanum* (as well as *D. asperispathum* and *D. grandispathum*) in having smaller seeds with a single dorsal ridge and a spathe usually wrinkled along the margins. *Dracontium asperispathum* also differs from *D. spruceanum* in having the inner spathe surface densely covered with translucent scales (vs. the inner spathe surface semiglossy in *D. spruceanum*). Finally, *D. grandispathum* differs from *D. spruceanum* in having a much larger spathe that is abruptly acuminate at the apex (45–50 cm long and 10–15 cm wide vs. 20–35 cm long and 3–6 cm wide and gradually acuminate for *D. spruceanum*).

Additional specimens examined. BRAZIL. **Amazonas:** basin of Rio Purus, Capoeira on Rio Cunhuá at Canahuá, *Prance et al. 16400* (INPA, NY, U, US); Benjamim Constant, Alto Solimões, *Duarte 6909* (MO, RB); Manaus, km 18 da BR-17, *Luiz 2996* (INPA, MG); Río Solimões, Tonantins, *Froes 12233* (NY). COLOMBIA. Caquetá, San Vicente del Caguán, Neiva-San Vicente, *Betancur et al. 1874* (COL). **Amazonas:** Río Amazonas, 2 km downriver from Puerto Nariño, *Plowman et al. 2412* (COL, ECON, GH); Mun. Leticia, PN Amacayacu, *Rudas et al. 3724* (MO). **Antioquia:** Maceo, hacienda Santa Bárbara, parcela de don Cipriano, Quebrada "Guarda sol," *Fonnegra et al. 7738* (HUA, K, MO, US); Corr. Providencia, above hydroelectric plant, *Soejarto & Villa 2750* (GH); Par. Nac. Nat. "Las Orquídeas," *Cogollo et al. 4063* (JAUM), *Cogollo et al. 3583* (JAUM); 2 km S of Chigorodó, *Haught*

4585 (COL); San Luís, Cañón del Río Claro, *Cogollo et al. 1455* (JAUM); Segovia, km 15 via Zaragoza Cerro Cabezas, Río Pocuné, *Cardona et al. 52* (COL). **Chocó:** Bolívar-Quibdó, km 67, *Grayum et al. 7638* (MO); Alto Río Baudó, Resguardo Indígena Emberá, *La Rotta 586* (COL); La Mojarra, near Istmina, *Juncosa 1307* (JAUM, MO); La Oveja-Quibdó, *Archer 1729* (US); Pueblo Rico-Istmina, Quebrada Antón, 15 km W of Santa Cecilia, *Croat 70886* (MO, TULV); Quibdó-Río Atrato, *Idrobo & Cuatrecasas 2685* (COL); Río Fujiadó, tributary of Río San Juan, *Forero et al. 4823* (COL). **Meta:** Honoria, Bosque Nac. Iparia, toward El Parrao, *Pittier 1775* (F); Río Duda near the mouth of Río Guayabero, *Pérez 7191* (COL); Llanos de San Martín, *Madison 848* (GH); La Serranía, Río Ariari at Aguasucia Lake, *Jaramillo 1036* (COL); Río Guatiquia, *André 1025* (K); Sabanas de San Juan de Arama, Río Ghejar, near Los Micos airport, *Idrobo 1193* (COL); Sierra de la Macarena, Caño Entrada, *Philipson 2203* (COL); Villavicencio, *Cuatrecasas 4633* (F, US), *Triana 289* (BM). **Nariño:** Fumaco, resguardo indígena Alto Albí, *M. S. González 125* (COL); Tumaco, Llorente, Albí, Cuasambí, *M. S. González 13* (COL). **Santander:** Landazuri, Cerro de Armas, 70 km N of Velez, *Fassett 25426* (NY, US); Puerto Berrio, *Haught 2203* (US); Barranca bermeja, *Haught 1575* (US). **Valle:** Cordillera Occidental, W slope, Río Sanquininí, La Laguna, *Cuatrecasas 15697* (F). **Vaupés:** Mitú, Río Vaupés, base of Cerro de Mitú, *Zarucchi 1916A* (COL); Mitú-Javareté, *Schultes & Cabrera 17184* (GH); Río Piraparaná Caño Teemeeña, *Schultes & Cabrera 17184* (GH). COSTA RICA. **Limón:** BriBri on Río Sixaola, Río Catarata, *Baker & Burger 111* (F, MO); Fila Carbón, 6 km E of Home Creek, *Hammel et al. 18119* (CR); Quebrada Mata de Limón, *Grayum et al. 4461* (MO); E of Puerto Viejo de Sarapiquí, *Grayum 4417* (MO); 2 km S of Manzanillo de Talamanca, *Grayum et al. 4388* (MO); Res. Indígena Talamanca, Amubri-Cachabri, *Chacón 1* (MO); 1.5 km above jct. of Río Urén and Río Sukut, *Herrera 3189* (CR). ECUADOR. **Manabí:** Machalilla Nat. Park near Puerto López, *Gentry & Josse 72402* (MO). **Napo:** 8 km E of Puerto Misahuali, *Hedin 144* (MO); Jatun Sacha, *Cerón 1046* (MO, QCNE); Limón Cocha, *Madison et al. 5343* (SEL); Nueve Rocafuerte, *Alarcon 62* (QCA); Reserva Faunistica Cuyabeno, Río Aguarico, *Palacios et al. 7660* (QCNE); Río Arajuno, Sola Cocha, *Neill et al. 6978* (F, MO, QCA); 6 km NNW of Ahuano, *Kohn 1193* (MO, WIS); Añangu, *Lawesson et al. 39334* (AAU); San José de Payamino, 40 km W of Coca, *Irvine et al. 968* (F); Res. Ecol. Antisana, Shamato, *J. L. Clark et al. 5014* (MO, QCNE); Hollín-Loreto, N of Archidona, *Whitten et al. 93091* (MO); Río Shiripuno, Huantime, *J. S. Miller & P. Yépez, Bai 562* (QCA); Laguna Limoncocha, *Jaramillo & Grijalva 11555* (QCA); Chiro Isla, Río Napo, *R. Bensmab 189* (QCA). **Pastaza:** Lorocachi, 3 km from Río Curaray, *Jaramillo et al. 30780* (AAU, MO); S of Río Curaray, mouth of Río Querano, *Neill & Palacios 6760* (MO); Mera, *Plowman 4490* (GH, S); 19 km S of Puyo, *Croat 50533* (MO, QCA). **Sucumbíos:** Parroquia Gonzalo Pizarro, 8 km SW of Recinto Amazonas, *Yánez & Shuigra 854* (QCA). **Zamora–Chinchipe:** between La Saquea and Yacuambí, 1 km N of Chapintza, *Harling & Andersson 23856* (GB); Pachicutza, trail to Hito, *Palacios et al. 8309* (MO). PANAMA. **Bocas del Toro:** trail to Quebrada Rabo de Puerco, *Santamaría et al. 803* (PMA); Santa Rosa on Río Changuinola, *G. Zhu 1503* (MO). **Coclé:** Distrito Olá, Potrero Llano-Volteadera via La Pintada and Llano Grande, 16 Feb. 2000, *Guerra & Wong 1036* (PMA); Alto Calvario, 5–7 km N of El Cope, *Thompson 4733* (CM). **Colón:** Guasimo, *Croat 9925* (MO); Santa Rita Ridge, *Croat 34334* (MO). **Darién:** upper Río Tuquesa, *Clezio 25* (MO). **Panamá:** Campo Tres, 3 mi. NE of Altos de Pacora, *Croat 22756* (MO); Altos de Pacora NE of Cerro Azul, *Dressler 4608* (PMA); Cerro Jefe area, *Dressler 3397* (PMA); Parque Nacional Altos de Campana, Serrania del Llorón, *Galdames et al. 4382* (PMA); El Llano–Cartí Rd., mi. 6–10, *Churchill 3824* (MO). **San Blas:** vic. Cangandí, *de Nevers & Herrera 5668* (MO); Cerro Brewster, *de Nevers et al. 6283* (MO); El Llano–Cartí rd., Nusagandí, *G. Zhu 1504* (MO); SW of Puerto Obaldía, *Croat 16799* (MO). **Veraguas:** Santa Fe area, N Alto de Piedra, *Croat 23126* (MO). PERU. **Amazonas:** Río Huampami, *Kayap 1327* (MO); Galilea, Río Santiago, *Berlin 3579* (MO); Quebrada Caterpiza, Río Santiago, 65 km N of Pinglo, *Huashikat 428* (MO); Río Cenepa, *Ancuash 129, 164* (MO); Huampami, ca. 5 km E of Chávez Valdivia, *Ancuash 1415* (MO). **Loreto:** Iquitos, Alpahuayo, *Vásquez 15226* (MO); Andoas, *Vásquez 3005* (MO); Yanamono Exp. Camp, 50 km by river from Iquitos, *J. P. Hedin & M. C. Hedin 107* (MO); Río Momon, trib. of Río Nanay, near Iquitos, *Gustafson 1972* (MO); Pto. Almendras, Yurimaguas, *Croat 17986* (MO); San Antonio, Río Itaya, *Jaramillo 3598* (MO); Río Macusari, *McDaniel 11018* (IBE). SURINAM. **Nickerie:** Nabij Kamp Koewinikreek, *Elias 17317* (BBS). VENEZUELA. **Amazonas:** 1 km S of San Carlos de Río Negro, *Liesner 9047* (MO, VEN).

Cultivated plants. Cult. Great Britain, Chelsea, William Bull's, *Carder s.n.* (K). Ecuador. Napo, Limón Cocha, 240 m, coll. by Madison, Plowman, and Besse, cult. at Kew (162-80-1627), from Selby 1978-2038, *Mayo 130* (K); Napo, cult. at MBG, from Selby 76-95-4, *G. Zhu 1499, 1490* (MO); Coca, 0°28′S, 76°58′W, cult. by B. Feuerstein, *Croat 75574, 75402*; *G. Zhu 1494, 1511* (MO); Limón Cocha, cult. at MBG, from Selby 78-2038, *G. Zhu 1448, 1486* (MO); Morona-Santiago, cult. by Betsy Feuerstein, vouchered as *Croat 78393* (MO); Zamora-Chinchipe, Pachicutza, 900 m, coll. by Henk van der Werff, Mar. 1994, *G. Zhu 1492* (MO); Pastaza, Mera, cult. at Selby Gardens (95-76-14), *Plowman 4490* (SEL), *Christenson 1102* (SEL), *Cobb 45* (SEL), *Madison 4176* (SEL not seen); Esmeraldas, 10 mi. N of Lita in July 1989, coll. by Morell, Hyndeman & Fisk, from J. Boos (West Palm Beach, Florida), cult. at Dewey Fisk's, Davie, Florida, *G. Zhu 1443* (MO).

23. Dracontium ulei K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 6: 115. 1914. TYPE: Brazil. Acre: near São Francisco & Alto Xapury, Oct. 1911, *E. Ule 9215* (holotype, B!; isotypes, B not seen, K!). Figure 27.

Tuber hemispherical or rarely rounded, 6–12 cm diam., 6–9 cm thick, flat above, rounded, white to brown below, 8–20 cm below ground level; tubercles few, rounded or cylindrically elongated, 0.5–1 × 1–1.5 cm, borne around the periphery of tuber; roots white, sometimes tinged pink above the tuber, to 2.5 mm diam.; *cataphylls* 1 (concealed from view soon after leaf development), 10–20 cm long, 1–2 cm wide, light brown, reaching or surpassing ground level. *Leaves* solitary; *petioles* 1–1.2 m long above ground, 2–4 cm diam. at midpoint, dark green tinged

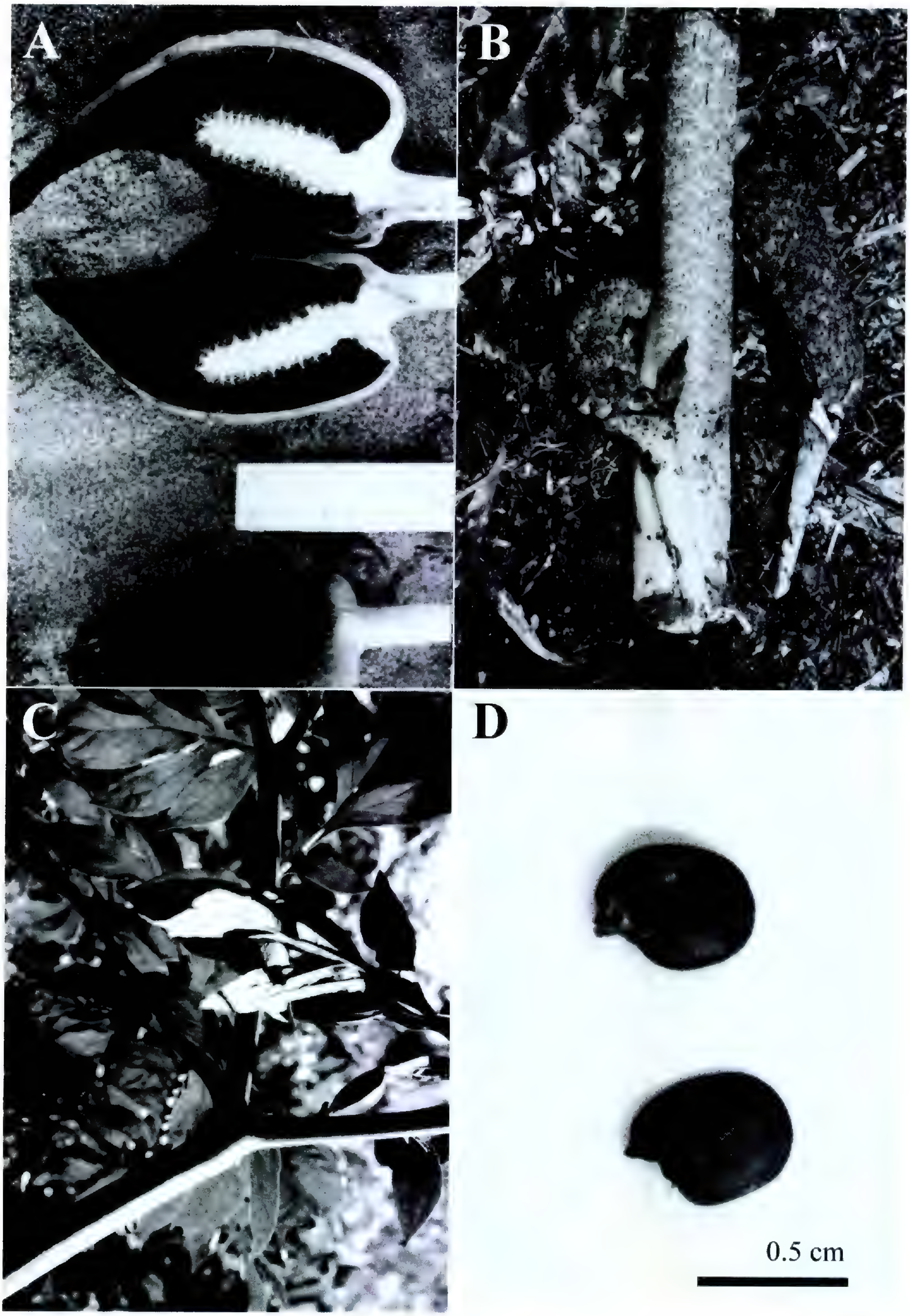

Figure 27. A–D, *Dracontium ulei*. —A. Two separate inflorescences, one in face view, one cut into two halves (*Nee 31734*). —B. Two infructescences with base of petiole, the inflorescence on the right with the spathe still persistent, the one on the left with loosening berries. —C. Leaf showing the three divisions of the blade (*Croat 85115*). —D. Seeds in lateral view (*Ule 9215*).

brown, contrastingly mottled with dirty white or pale green blotches and forming a reptilian pattern, usually smooth in upper half and with irregular protuberances in lower half; juvenile blade sagittate, or sagittately lobed; mature *blades* ascending to 45° to the petiole (often), 0.8–1 m diam., papyraceous, rarely fenestrate, never variegated, with abundant raphide cells and often dark markings, glossy and medium green above, glossy and dark green below; *middle division* twice trichotomously branched, 50–60 × 50–55 cm, with terminal subdivision consisting of 3 sections, with each basal subdivision consisting of many segments; lateral divisions twice dichotomously branched, 50–65 × 55–60 cm, with terminal subdivision consisting of 2 sections, with basal subdivision consisting of many segments; terminal and subterminal sections free; leaf segments often entire, broadly oblanceolate, more than 5 cm wide on each side of the major ribs, oblanceolate, mostly free from each other in each division, often with contrastingly smaller rounded or triangular segments alternating with larger segments; apices acuminate; *ultimate segments* 10–15 cm long, often free from penultimate segments; other segments 3–8 cm long; penultimate segments free from subterminal sections; medial segments free from basal subdivisions; basal segments present, free from each other; rachises patterned distinct from petiole, pale green, smooth; tertiary veins obscure above and weakly raised below; *bracteoles* 2 or 3, 8–20 × 1–2 cm, pink, the longest one ± as long as the peduncle, reaching the spathe. *Inflorescence* solitary, appearing before new leaf; *peduncle* 8–20 cm long above ground, 0.6–0.8 cm diam. at midpoint, often almost completely subterranean, scarcely mottled, whitish tinged pink, smooth; *spathe* 6–10 cm long, 3–4 cm wide, non-cymbiform, constricted at a certain point and differentiated into a proximal tube and a distal lamina (blade), cucullate, arching 45°–90°, apex acuminate; 4–6 × 3–4 cm at widest point; lamina shorter than the tube; inner surface covered with dense, translucent scales to 1 mm long, violet-purple, with translucent area obscure; outer surface maroon tinged brown, matte; margins entire, broadly overlapping in the lower two-thirds; veins obscure inside and outside, similar to the spathe in color; *spadix* hidden, stipitate, cylindric, brown-purple, 3–4 cm long, 1.2–1.4 cm diam. at anthesis, never with appendages at apex; stipe 0.4–0.5 cm long, 0.5 cm diam. at anthesis. Flower tepals 4 to 6, 2–3 mm long, 1–1.5 mm wide, light brown; stamens 4 to 6; filaments 1.5–4 mm long; anthers 0.8 mm long (elliptic), completely exserted; ovary incompletely 3- or 4-locular, white; stigma 3- or 4-lobed; style 1–1.5 mm long above tepals, brownish purple, persistent. *Infructescence* with spadix 6–7(–10) cm long, 1.5–2(–3) cm diam. in fruit; *berries* 2-seeded, young berries 0.4–0.5 cm diam., 0.5–0.7 cm thick, obliquely obovoid, apically subtruncate; young berries medium green; mature berries color unknown, with abundant raphide cells; *seeds* 0.4–0.5 cm diam., reniform, reddish brown, laterally raised, smooth; dorsal ridges obscure.

Phenology. Flowering in early September; young infructescences collected in October and mature fruits in October.

Distribution and habitat. *Dracontium ulei* ranges from Acre, Brazil, to Pando, Bolivia. It occurs in the *Tropical moist forest* (T-mf) life zone (Holdridge et al., 1971), at 125–230 m.

Local names. "Milho de cobra" (*Lowrie et al. 592*, NY).

Discussion. *Dracontium ulei* is characterized by its usually subterranean peduncle and inner surface of the spathe densely covered with translucent scales. It is easily confused with *D. bogneri*, which shares a cucullate spathe covered inside with translucent scales. However, *D. bogneri* has seeds laterally depressed with 3 obvious dorsal ridges (vs. laterally raised with obscure dorsal ridges for *D. ulei*). *Dracontium ulei* is also close to *D. dubium* and *D. purdieanum*, but can be distinguished by its spadix concealed at anthesis and deeply hooded spathe with small scales to 1 mm long on the inner surface. The latter two species differ by having the spadix exposed at anthesis and a spathe that is not hooded and lacks scales this small on the inner surface.

Additional specimens examined. BOLIVIA. **Pando:** Río Madre de Dios, Sena, *Nee 31734* (MO, NY). BRAZIL. **Acre:** Rio Branco-Brasília, km 16, *Nelson 752* (MG, MO, R); Rio Caete, 12 km above mouth, *Prance et al. 7925* (NY, US); Rio Branco-Xapury, BR 317, km 16, *Cid & Souza 2987* (MG, MO); Rio Branco-Sena Madureira, km 40, *Cid & Souza 3022* (NY); Assis Brasil, basin of Rio Purus, upper Rio Acre, *Daly et al. 9820* (NY).

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APPENDIX 1. List of species.

1. *Dracontium amazonense* G. Zhu & Croat
2. *Dracontium angustispathum* G. Zhu & Croat
3. *Dracontium asperispathum* G. Zhu & Croat
4. *Dracontium asperum* K. Koch
5. *Dracontium bogneri* G. Zhu & Croat
6. *Dracontium croatii* G. Zhu
7. *Dracontium dubium* Kunth
8. *Dracontium gigas* (Seem.) Engl.
9. *Dracontium grandispathum* G. Zhu & Croat
10. *Dracontium grayumianum* G. Zhu & Croat
11. *Dracontium guianense* G. Zhu & Croat
12. *Dracontium longipes* Engl.
13. *Dracontium margaretae* Bogner
14. *Dracontium nivosum* (Lem.) G. Zhu
15. *Dracontium peruvianum* G. Zhu & Croat
16. *Dracontium pittieri* Engl.
17. *Dracontium plowmanii* G. Zhu & Croat
18. *Dracontium polyphyllum* L.
19. *Dracontium prancei* G. Zhu & Croat
20. *Dracontium purdieanum* (Schott) Engl.
21. *Dracontium soconuscum* Matuda
22. *Dracontium spruceanum* (Schott) G. Zhu
23. *Dracontium ulei* K. Krause

APPENDIX 2. Index to exsiccatae. Type species in boldface.

R. Aguilar 1976 (16); R. Aguilar & V. Guzmán 2849 (16); Alarcon 62 (22); P. Alcorn & J. Mallet 8 (15); P. Allen 3427 (21), 5318 (16); Alson 971 (18), 1107 (18); E. Ancuash 129 (22), 164 (22), 1415 (22); André 1025 (22); Anonymous s.n. in 1889 (8), s.n. (8); T. Antonio 3736 (22); Archer 1729 (22); Aristeguieta 5381 (7), 12734 (7), s.n. (20); Asplund 19281 (22), 19588 (22); M. Aulestia 1823 (9); Aymard & Stergios 3807 (7).

Baker & Burger 111 (22); Balée 2106 (18), 3476 (14); P. Barbour 5817 (17); A. Barfod 41597 (6); Barnes s.n. (4), 18584 (4); Barret s.n. (4); Bartlett & Lasser 16831 (21); J. Beach 1490 (8); R. Bensmab 189 (22); Betancur et al. 1874 (22); Berlin 2034 (22), 3579 (22); G. Black 47-2084 (14), 18814 (14); Bogner s.n. (2), s.n. (21), 1132 (19), 1267 (8), **2097 (5);** Boos s.n. (TRIN 31296) (4); Bosbeheer 9845 (18); Britton & Britton 10060 (4); Broadway 407 (18), 5212 (4), 7455 (4), 7926 (4), 9214 (4); N. E. Brown s.n. in 1878 (8), **s.n. (8),** s.n. in 1881 (8), s.n. in 1883 (8); W. Bull s.n. (8); Bunting 2856 (7), 3677A (7), **3677B (7),** 4432 (7); Bunting & Trujillo 2221 (7), 2222 (7), 2223 (7), 2224 (7), 2225 (7); Bunting et al. 10866 (20); Burger & Baker 9999 (8), 10131 (16); Burger & Gentry 9017 (16); Burger & Stolze 5551 (16), 5800 (8), 5845 (8), 9017 (16); Burger et al. 10587 (16), 12266A (16), 12266B (16).

Callejas et al. 4166 (22); D. Cárdenas 1805 (10); Carder s.n. (22); Cardona et al. 53 (22); Castillo 260 (7); E. Catharino et al. 1832 (13); Cerón 1046 (22), 3598 (22); Cerón & M. Cerón 3070 (9), 4687 (22); Chacón 1 (22), 1414 (21); Christenson 1102 (22), 1154 (6), 1287 (17), 1490 (17), 1491 (17), 1576 (6); H. W. Churchill 3824 (22); Cid & Souza 2987 (23), 2988 (23), 3022 (23); J. L. Clark et al. 5014 (22); Clezio 25 (22); Cobb 45 (22); Cogollo et al. 1455 (22), 1497 (22), 1524 (22), 3583 (22), 4063 (22); Cornejo 1520 (17); Cowan 38843 (18); Cremers 7682 (18), 11618 (18), 12734 (18), 12737 (18); Cremers & Crozier 14308 (18); T. B. Croat 9925 (22), 12246 (21), 16799 (22), 17986 (22), 19391 (3), 20550 (3), 22756 (22), 23126 (22), 27217 (22), 27794 (21), 27795 (21), 34334 (22), 35104 (16), 36370 (8), 50533 (22), 53539 (15), 53561 (1), 56898 (1), 62349 (12), 68381 (8), 70886 (22), 71785 (18), 71798 (6), 71840 (8), 71895 (1), 72368 (6), 73040 (6), 73867 (19), 73989 (17), 74210 (18), 74284 (18), 75402 (22), 75574 (22), 78393 (22), 85115 (23), 85460 (12); T. B. Croat & Grayum 59844 (16); T. B. Croat & D. Hannon 79217 (16); Cuatrecasas 4633 (22), 15697 (22), 16474 (10); Curran 349 (20).

Daly et al. 9820 (23), 10000 (12); Davidson 8624 (8); **Davidson & Jones 9605 (1);** Delascio 6818 (7); Deward 67 (18), 88 (18); A. T. G. Dias 513 (18); C. Díaz et al. 1164 (3); C. W. Dodge 5622 (8); Dodson 5951 (6), 7288 (6); Dodson & Fallen 7762 (6); Dodson et al. 17756 (9); Donselarr 1159 (4); **Dressler s.n. (21),** 3397 (22), 4286 (22), 4608 (22); Duarte 6909 (22); Dugand 1161 (20); J. Duke 5103 (10).

Elburg 9845 (18); Elias 17317 (22); **Emmerich 4053 (13),** 4598 (13).

Fantz 4115 (21), 4249 (21); Fassett 25426 (22); Feuillet 3993 (18); Fleury 802 (18); Florschutz & Maas 3162 (4); Foldats 216A (7); Folsom 4583 (10), 5740 (22); Forero et al. 3800 (10), 4718 (10), 4823 (22); R. B. Foster 1724 (22), 4389 (2), 6978 (12), 7212 (17), 9558 (17); Foster et al. 3422 (17); Froes 12233 (22).

C. Galdames et al. 4382 (22); Garcia et al. 1527 (21); Garwood 1639A (21); Gély 60 (18), 234 (14); Gentry 2598 (21); Gentry & Daly 18798 (15); Gentry & L. Emmons 38721 (3); Gentry & C. Josse 72402 (22); Gentry & P. Núñez 69383 (17); Gentry & Ortiz 74202 (3); Gentry et al. 25597 (15), 29076 (3), 30026 (15), 37215 (3), 42629 (3), 51147 (17), 52159 (15), 54686 (3), 78072 (17); Ginzberger s.n. (16), 3109 (14); Girardi 16 (7); Gómez 18513 (8), 22029 (16), 22935 (16); E. Gonçalves 97 (13); González 13 (22); Gragson & Gragson 4 (13), 13 (13); C. Grández et al. 2629 (15); **de Granville & Cremers 1129 (11)**; Grayum 7992 (8), 7911 (8); Grayum et al. 4388 (22), 4461 (22), 6046 (16), 7638 (22); Grenand 1277 (11), 1913 (18); C. Guerra & B. Wong 1036 (22).

Hahn et al. 17 (2); Hallé 790 (18); Hammel 11764 (8); Hammel & D'Arcy 6364 (22); Hammel & Wilder 17283 (9); Hammel et al. 15204 (16), 18119 (22); Harling & Andersson 16404 (9), 23856 (22); Hassler 10960 (13); Haught 1575 (22), 1741 (22), 2203 (22), 4585 (22); Haxaire 1757 (2), 2877 (2); J. Hedin 144 (22); Herrera 252A (10), 3189 (22), 4529 (16); W. S. Hoover et al. 3279 (6); Hoyos & Hernandez 241 (22); Huber 1826 (7), 1826-1 (7), 2036 (14), 3667 (14); Huashikat 428 (22).

Idrobo 1193 (22); Idrobo & Cuatrecasas 2685 (22); Inchaustegui s.n. (2); Irvine et al. 968 (22); **Irwin 55045 (4)**; Irwin et al. 34730 (5), 55749 (4).

Jaramillo 1036 (22), 3598 (22), 4938 (22); Jaramillo et al. 30780 (22); Jácome 399 (22); Jacquemin 2191 (18), 2194 (18); Jenman 491 (4), 6895 (4); Jimenez 3420 (4); Jipa et al. 968 (9); Johnson 243 (4); de Jong 20 (15); Juncosa 1307 (22).

Kalloo & Gonzales 1358 (4); Kastelein 16153 (18); R. Kayap 898 (22), 1327 (22); Kennedy 1646 (16); C. Kernan & P. Phillips 648A (16); Killip & Smith 29351 (2); King 416 (2); **Klug 254 (2);** Knapp & Mallet 7210 (15); Koch s.n. (4); Kohn 1193 (22), 1210 (22); Kress 76585 (16); Krukoff 4987 (15); Kugikat 1132 (16).

La Rotta 586 (22); Larpin 998 (18); J. E. Lawesson et al. 39334 (22); Lehmann 246619 (8); Leprieur s.n. (18); Leveau 222 (22); R. Liesner 2017 (16), 2867 (16), 9047 (22); R. Liesner & A. González 5773 (7), 13060 (20); R. Liesner et al. 2720 (21), 2765 (21); R. Lima 108 (14); Lindeman 4608 (18); Liogier 19363 (4); Lister 461 (7); Lobato et al. 60 (14); B. Løjtnant & U. Molau 13549 (9); Lowrie et al. 530 (23), 592 (23); Luteyn 3394 (21), 4050 (22), 16831(21); Luteyn et al. 9021 (9); Luiz 2996 (22).

Maare 189 (3); P. J. M. Maas et al. 8299 (1), 13201 (12); Machiel & Rosário 534 (14); Madison 848 (22), 3764 (21), 4140 (6), 4176 (22), 4229 (17); Madison et al. 5343 (22); Marín 285 (16); Martin & Lau-Cam 1315 (2); Martinelli et al. 6815 (18); Martius 282 (14); **Matuda 17780 (21)**; Mayo 130 (22); McAlpin 85-34 (16); McDaniel 11018 (23); Meier 435 (7); Milliken 1717 (4); Milliken et al. 511 (19); J. F. Morales 546 (16); Moretti 122 (18); Mori 1850 (22); Mori & Kallunki 2590 (22); Mori et al. 9666 (18).

Nee 31734 (23); D. Neill 4336 (8), 8713 (22); D. Neill & W. Palacios 6760 (22); D. Neill & Vincelli 3512 (8); D. Neill et al. 6978 (22), 8160 (3); C. Nelson 752 (23); G. de Nevers & H. Herrera 5668 (22); G. de Nevers et al. 6283 (22); Nicolson 1119 (18); P. Nuñez 1885 (17).

Ortega 748 (7); Ortega & Aristeguieta 1554 (7).

W. Palacios 1654 (22), 4242 (9); **W. Palacios et al. 311 (9),** 7660 (22), 8309 (22); Paris 36 (18); Pérez 7191 (22); Pesha 5 (17); Philipson 2203 (22); Pinkley 60 (9); Pipoly 15612 (3); Pipoly et al. 12535 (3), 13282 (3); J. M. Pires 6594 (14); Pittier 1775 (22), 3429 (21), 3650 (21), 4232 (22), 6546 (10), 9232 (22), 11985 (16); **Pittier & Tonduz 7515 (16)**; Plowman 4490 (22), 10926 (6), 12043 (5); Plowman & Davis 4490 (22), 5054 (17), **5054 (17)**; Plowman & Kennedy 5654 (17); Plowman & Martin 1661 (3); Plowman & Schunke V. 11536 (15); Plowman et al. 2412 (22), 6720 (2), 6728 (3), **6729 (3),** 6815 (2), 6820 (3), 8616 (18), 9895 (14), 12510 (1), 12550 (1); Proctor 46104 (4), 46460 (4), 47976 (4), 48044 (4), 48047 (4); Prance et al. 7925 (23), 16400 (22), **28732 (19);** Pulle 161 (18); **Purdie s.n. in 1845 (20).**

F. Quesada 259 (16).

Rentería 4220 (10); Rentería & Cardenas 4314 (10); Rentería et al. 4212 (10); Richard s.n. (18); Riera 415 (18); Rimachi 4043 (15), 5304 (15); Rodriguez 158 (7); Roig 11 (8); R. Romero 6357 (10); Rudas et al. 3724 (22); R. Rueda et al. 2869 (8), 3295 (8), 3390 (8), 5225 (8), 8615 (8), 10190 (8).

Sagot 608 (18); Salick 7370 (15); Sang 16866 (18); Santamaria et al. 803 (22); Saunders 1920 (4); Sauvain 175 (18); Schultes 14799 (2); Schultes & Cabrera 17184 (22); Schultze-Rhonhof 2998 (22), 3031 (22); Schunke-Vigo 1775 (15), 6428 (15), 7140 (15); Shank & Molina 4953 (8); A. C. Smith 3029 (4); Soejarto & Villa 2750 (22); J. Solomon 5334 (8); **Spruce 2406 (22);** Stahel s.n. (18); Standley & Valerio 48885 (8), 49002 (8); B. Stein et al. 3999 (2); Stergios & Delgado 12940 (18); Stern et al. 93 (10); W. D. Stevens 7007 (8); Steyermark 131646 (7); Steyermark et al. 117171 (7), 127097 (7), 131647 (7); Strudwick et al. 3987 (18); Susach 251 (13); Sytsma et al. 4269 (22).

Tamayo 3188 (1); Thompson 4658 (22), 4686 (22), 4733 (22), 4821 (22); I. Thurn s.n. (4); Tina & Tello 2054 (3); Treacy & Alcorn 198 (2); Triana 289 (22), 691 (22); Trujillo 12633 (13).

Ule 5272 (12), 5286 (1), **5781 (12), 9215 (23);** Utley & Utley 671 (22).

Valerio 24 (8), 678 (8); C. Vargas 13433 (17); R. Vásquez & N. Jaramillo 3598 (15), 4938 (2), 7595 (2), 8562 (15), **15226 (15),** 16094 (3), 16524 (2); R. Vásquez et al. 3005 (22), 4838 (2), 4841 (17), 6761 (2), 8081 (2).

Whitten et al. 93091 (22); Williams 155 (3), 827 (2), 1750 (3), 1942 (3), 2119 (3), 3756 (2), 4631 (15), 5144 (22), 7916 (15); Woodbury s.n. (4); Wullschlaegel 1096 (4); Wurdack & Monachino 41392 (7).

A. Yanez & Shuigra 854 (22); R. Young 189 (17).

Zarucchi 1459 (22), 1916A (22); G. Zhu 1154 (8), 1155 (8), 1156 (8), 1157 (8), 1158 (8), 1159 (8), 1440 (18), 1441 (18), 1442 (4), 1443 (22), 1444 (4), 1445 (4), 1446 (17), 1447 (17), 1448 (22), 1453 (6), 1454 (1), 1455 (19), 1456 (1), 1457 (1), 1458 (19), 1459 (6), 1460 (1), 1461 (1), **1462 (18),** 1463 (19), 1464 (1), 1465 (1), 1466 (17), 1467 (8), 1478 (4), 1479 (4), 1480 (17), 1481 (8), 1482 (17), 1483 (18), 1484 (4), 1485 (21), 1486 (22), 1487 (17), 1488 (18), 1489 (1), 1490 (22), 1492 (22), **1493 (6),** 1494 (22), 1495 (6), 1496 (17), 1496A (17), 1497 (4), 1498 (17), 1499 (22), 1501 (19), 1509 (4), 1510 (5), 1511 (22), 1512 (17), 1513 (18), 1514 (1), 1515 (4), 1516 (1), 1517 (8), 1518 (6), 1533 (13), 1580 (6); G. Zhu & T. B. Croat 1503 (22), 1502 (21), 1504 (22), **1506 (10),** 1507 (10); G. Zhu et al. 1505 (22).

REVISION OF *DIEFFENBACHIA* (ARACEAE) OF MEXICO, CENTRAL AMERICA, AND THE WEST INDIES[1]

Thomas B. Croat[2]

Abstract

The genus *Dieffenbachia* Schott has approximately 135 species, most of them occurring in South America. Major centers of diversity for the genus include Colombia with 37 species, Ecuador (34), Peru (30), Brazil (27), Panama (20), and Costa Rica (13). There are 26 species in Central America, with 20 species (77%) new to science. These are *D. burgeri* Croat & Grayum, *D. copensis* Croat, *D. crebripistillata* Croat, *D. davidsei* Croat & Grayum, *D. fortunensis* Croat, *D. fosteri* Croat, *D. galdamesiae* Croat, *D. horichii* Croat & Grayum, *D. isthmia* Croat, *D. killipii* Croat, *D. lutheri* Croat, *D. nitidipetiolata* Croat, *D. obscurinervia* Croat, *D. panamensis* Croat, and *D. standleyi* Croat described herein and *D. beachiana* Croat & Grayum, *D. concinna* Croat & Grayum, *D. grayumii* Croat, *D. hammelii* Croat & Grayum, and *D. tonduzii* Croat & Grayum described elsewhere. Most species range from Nicaragua to Panama. Belize has only 1 species of *Dieffenbachia*; Mexico, El Salvador, and Guatemala have 2 species, followed by Honduras (3), Nicaragua (6), Costa Rica (13), and Panama (20). Only a few Central American species could be considered widespread. Among the most widespread are *D. oerstedii* Schott and *D. wendlandii* Schott, both of which range from Mexico to Panama, as well as *D. nitidipetiolata* and *D. tonduzii*, which range from Honduras to Ecuador. Species endemism is high, especially in Costa Rica (3) and Panama (9). A total of 9 species are shared between Panama and Costa Rica. Eight species, almost 31% of the total, range into South America. These are *D. davidsei*, *D. isthmia*, *D. killipii*, *D. longispatha*, *D. nitidipetiolata*, *D. obscurinervia*, *D. seguine*, and *D. tonduzii*. Most of these only extend to Colombia, but three species, *D. killipii*, *D. nitidipetiolata*, and *D. tonduzii*, range to Ecuador. Only *D. killipii* ranges to the eastern slope of the Andes. *Dieffenbachia seguine* ranges into Brazil and Bolivia, from the West Indies.

Key words: Araceae, Central America, *Dieffenbachia*, Mexico, South America, West Indies.

The family Araceae is worldwide in distribution, but most species occur in tropical areas. Its centers of distribution include both Asia and America (Croat, 1979), with 31 genera in the Americas and 28 found in Asia. There are 16 genera in Africa, Madagascar, and the Seychelles. A few genera are restricted to temperate regions of the Northern Hemisphere, including the Mediterranean region (*Calla* L., *Lysichiton* Schott, *Orontium* L., *Peltandra* Raf., *Symplocarpus* Salisb. ex Nutt.), including the Mediterranean region (*Arisarum* Mill., *Ambrosina* Bassi, *Arum* L., *Dracunculus* Mill., *Helicodiceros* Schott ex K. Krause). Important local centers of generic endemism in the family include Brazil, which has four endemic genera (*Bognera* Mayo & Nicolson, *Dracontioides* Engl., *Gearum* N. E. Br., *Zomicarpa* Schott), and the Indomalaysian region, with 14 endemic genera. At least 2550 species, representing four-fifths of the total, occur in the Neotropics. The Central American flora comprises 19 genera within the Araceae.

With an estimate of more than 2550 species in Latin America, the Araceae are one of the largest families of flowering plants in the region. Yet no

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other family is so poorly known taxonomically. Plants exhibit considerable morphological plasticity at all stages of development. Many of the genera, especially the hemiepiphytic genera *Rhodospatha* Poepp., *Monstera* Adans., and *Syngonium* Schott, exhibit complex patterns of heterophylly, with drastically different morphology at different stages of development (Croat, 1981 [1982]; Ray, 1981, 1987). Most members of the family have succulent parts, making them difficult to collect and preserve.

Dieffenbachia is one of several medium-sized genera in the Araceae, with an estimated 135 species. This revision is the first major review of *Dieffenbachia* for Central America since Adolf Engler's (1915) generic treatment in *Das Pflanzenreich*. *Dieffenbachia* is one of the most important genera of understory herbs in the family, and it is often a dominant component of humid to wet tropical forests, especially from sea level to 1500 m. It inhabits life zones ranging through *Premontane moist forest* (P-mf), *Tropical moist forest* (T-mf), *Premontane wet forest* (P-wf), *Tropical wet forest* (T-wf), and *Premontane rain forest* (P-rf) (Holdridge, 1967). While most species occur in virgin humid forests, the genus is known from freshwater swamps, stream banks, regrowth forest, among rock outcrops, and occasionally on road banks. It often constitutes the most conspicuous element of the understory vegetation because of its abundance, frequent colonial growth habit, and generally large, showy leaves. The genus provides a wide variety of choice ornamental plants for horticulture, including most of the species treated here.

The genus is distinct and not easily confused with any other aroid. It is closest to *Bognera*, which differs in lacking staminodia surrounding the pistillate flowers and in having higher-order venation reticulate. In contrast, *Dieffenbachia* has several staminodia surrounding the pistils and higher-order venation parallel-pinnate. However, the monotypic genus *Bognera* is endemic to Brazil, and it is not likely to be a problem with determination of most *Dieffenbachia*. Alternatively, *Dieffenbachia* is frequently confused with *Philodendron* Schott, particularly the terrestrial species of the latter with non-cordate blades. *Philodendron* species are mostly hemiepiphytic, rarely terrestrial as is *Dieffenbachia*. Even when *Philodendron* species are terrestrial and have non-cordate blades, they can be distinguished by the remotely many-flowered pistils that are not surrounded by staminodia, as well as the lack of the acrid foul-smelling, irritating sap that is so closely associated with *Dieffenbachia*.

Species diversity of *Dieffenbachia* shows a general diminution from Mexico to Middle America with the lowest totals just north of the San Juan depression (Nicaragua), followed by a marked increase approaching the South American continent. (In this treatment, Central America is defined as all the area between Mexico and Colombia, whereas Middle America is all the area between Mexico and Panama.) Mexico has 2 species, Guatemala (2), Belize (1), Honduras (3), El Salvador (2), Nicaragua (6), Costa Rica (13), and Panama (20) (Table 1). Endemism is high, especially in Costa Rica with 3 endemic species and Panama with 9. A total of 7 species are shared between Panama and Costa Rica. Just under one-third (31%) of Central American species of *Dieffenbachia* range into South America, these being *D. davidsei*, *D. isthmia*, *D. killipii*, *D. longispatha*, *D. nitidipetiolata*, *D. obscurinervia*, *D. seguine*, and *D. tonduzii*.

Materials and Methods

This revision is based on more than 29 years of field studies in Central and South America, between 1967 and 1996. All but one species were studied live in the field or under cultivation at the Missouri Botanical Garden. The descriptions have been prepared from both living and dried specimens. The exception is *D. fosteri*, where the description was based solely on the type specimen. The use of ("dried") preceding all or any part of the description is an indication that all that follows is based on herbarium material only. Morphological characters were coded directly into a computerized database to ensure parallel and sortable descriptions. The aroid descriptions database contains 784 character states applicable to the morphological diversity expressed in *Dieffenbachia* (Croat, 1997). Discussions and references to illustrations, as well as exsiccatae, are stored separately, but tied to a particular species description and to the nomenclatural information by a unique taxon number. Terminology and usage in the descriptions in this revision are largely defined by Croat and Bunting (1979) and elaborated in Croat (1997).

Ecological zones, though sometimes estimated from my own experience with Central American vegetation, are largely taken from Holdridge life-zone maps (Holdridge, 1967; Holdridge et al., 1971), where they exist for Central American countries, and for Mexico from the "Mapa de tipos de vegetación de la República de México" (Flores et al., 1971).

Herbarium material has been widely distributed and original field vouchers are cited for all herbaria whose material was seen (see Appendices 1, 2). Herbarium material may consist of one of three

Table 1. Distribution and endemism in *Dieffenbachia* species from Mexico, Central America and the West Indies. X = species present; E = endemic species.

Species	Country													
	Mexico	Guatemala	Belize	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	West Indies	Colombia	Ecuador	Venezuela	Brazil	Bolivia
D. aurantiaca							X	X						
D. beachiana							X	X						
D. burgeri							E							
D. concinna						X	X							
D. copensis								E						
D. crebripistillata								E						
D. davidsei							X	X		X				
D. fortunensis								E						
D. fosteri								E						
D. galdamesiae								E						
D. grayumiana							X	X						
D. hammelii							E							
D. horichii							E							
D. isthmia								X		X				
D. killipii							X	X		X	X			
D. longispatha								X		X				
D. lutheri								E						
D. nitidipetiolata							X	X	X		X	X		
D. obscurinervia								X		X				
D. oerstedii	X	X	X	X	X	X	X	X						
D. panamensis								E						
D. pittieri								E						
D. seguine									X	X	X	X	X	X
D. standleyi					X	X								
D. tonduzii						X	X	X		X	X			
D. wendlandii	X	X		X	X	X	X	X						
Total number of species (percent of endemics)	2	2	1	2	3	6	13 (23%)	20 (40%)	1	8	4	1	1	1

kinds: (1) complete original sets (wild collected); (2) sterile original material with an inflorescence added from a cultivated plant of the same number; and (3) material collected entirely from the cultivated plant. Specimens based entirely or in part on cultivated material are clearly indicated on the herbarium label.

Herbarium specimens were borrowed from most major herbaria including: A, AAU, B, BBS, BM, BR, CAS, CAY, CHOCO, CM, COL, CR, CUVC, DAV, DS, DUKE, EAP, ECON, ENCB, F, FLAS, FSU, FTG, G, GH, GOET, GUAY, HBG, HUA, INB, ISC, K, L, LA, LL, M, MEXU, MICH, MY, NY, P, PMA, PORT, QAP, QCA, QCNE, RSA, S, SCZ, SEL, STRI, TEFH, TEX, TULV, U, UC, UMO, US, USC, USJ, VEN, and WIS. Unless specifically designated as not seen, all specimens are to be presumed to have been examined personally.

Data on the living collection of *Dieffenbachia* are computerized, and the entire collection, including many South American species that are being described separately, undergoes regular inventories to include events such as flowering time and attempted hybridizations. This allows electronic access to information on status, location, flowering dates, the number of vouchers prepared, and the status of the description. All specimens cited have been recorded in a computerized database for permanent referral. See www.mobot.org.

History of the Genus *Dieffenbachia*

Heinrich Wilhelm Schott

The genus *Dieffenbachia* was described in 1829 by H. W. Schott (Schott, 1829). Schott based the genus on a single species, *Caladium seguinum* (Jacq.) Vent. (Ventenat, 1800), previously described as *Arum seguine* Jacq. (Jacquin, 1763) as well as

Table 2. Treatment of *Dieffenbachia* species by H.W. Schott (1860).

Species treated by H. W. Schott (1860)	Origin	Synonymizations as treated by Engler (1915)
1. *D. cognata* Schott	Suriname	= *D. seguine* var. *lineata* (Mart. ex Schott) Engl.
2. *D. consobrina* Schott	Brazil	= *D. seguine* var. *viridis* Engl.
3. *D. costata* H. Karst. ex Schott	Venezuela	
4. *D. gollmeriana* Schott	Venezuela	= *D. seguine* var. *viridis* Engl.
5. *D. humilis* Poepp.	Peru	
6. *D. irrorata* Mart. ex Schott	Brazil	= *D. seguine* var. *lingulata* (Mart.) Engl. subvar. *irrorata* (Mart.) Engl.
7. *D. lineata* K. Koch & Bouché	New Granada	= *D. seguine* var. *lineata* (K. Koch & Bouché) Engl.
8. *D. lingulata* Mart. ex Schott	Brazil	= *D. seguine* var. *lingulata* (Mart. ex Schott) Engl.
9. *D. liturata* Schott	Unknown	= *D. seguine* var. *liturata* (Schott) Engl.
10. *D. macrophylla* Poepp.	Peru	
11. *D. neglecta* Schott	Jamaica	= *D. seguine* var. *viridis* Engl.
12. *D. obliqua* Poepp.	Peru	
13. *D. oerstedii* Schott	Central America	
14. *D. picta* Schott	Unknown	
15. *D. plumieri* Schott	Martinique	= *D. seguine* var. *viridis* Engl.
16. *D. poeppigii* Schott	Peru	= *D. seguine* var. *viridis* Engl.
17. *D. robusta* Schott	Unknown	
18. *D. seguine* (Jacq.) Schott	Martinique	
19. *D. spruceana* Schott	Brazil	= *D. humilis* Poepp.
20. *D. ventenatiana* Schott	Suriname	= *D. seguine* var. *ventenatiana* (Schott) Engl.
21. *D. wendlandii* Schott	El Salvador	= *D. seguine*

by Linnaeus (1763). The next species described were three from Peru (Poeppig, 1845), *D. humilis* Poepp., *D. macrophylla* Poepp., and *D. obliqua* Poepp.

Between 1852 and 1864 an additional 18 species were described, all but 4 of them by H. W. Schott. Of these only 3 were recognized in Engler's (1915) revision, while the remainder were synonymized or recognized at the subspecific level, mostly under *Dieffenbachia seguine*. Those recognized at the specific level were *D. picta* Schott, *D. costata* H. Karst. ex Schott, and *D. oerstedii* Schott. Between 1866 and 1878, 12 species were described, with 6 more of these being recognized as distinct in Engler's revision (Table 3). The first major revision of the genus was that of Schott (1860) in his *Prodromus Systematis Aroidearum*, treating 21 species, of which Engler later (1915) recognized only 7 (see Table 2).

ADOLF ENGLER

The next revisionary effort made with *Dieffenbachia* was by Engler (1878) in the treatment of the Araceae in Martius's *Flora Brasiliensis*. In this treatment 3 species were included and 16 new combinations made (these within *D. seguine* and *D. picta*). A year later, in his treatment of *Dieffenbachia* in DeCandolle's *Monographiae Phanerogamarum* (Engler, 1879), 6 species were treated and 2 more combinations were made. Between 1879 and 1899, 14 additional species were described, only 3 of which were recognized by Engler in 1915. These were *D. daguensis* Engl., *D. enderi* Engl., and *D. olbia* L. Linden & Rodigas.

In 1899, Engler produced another small work on *Dieffenbachia* in which he treated 19 species and made 24 new combinations, but provided no descriptions except for one new species, *Dieffenbachia aurantiaca* Engl. Only 9 species were described between this work (1899) and Engler's (1915) revision. Those taxa still recognized by Engler (1915) were *Dieffenbachia cordata* Engl., *D. weberbaueri* Engl., *D. gracilis* Huber, and *D. cannifolia* Engl. ex Ule.

The last revision of the genus *Dieffenbachia* was by Engler (1915) in *Das Pflanzenreich*. This revision contained both keys and descriptions for 27 species. A total of 11 new combinations were made and 6 new species described (see Table 3). The new species were *D. aglaonematifolia* Engl., *D. brittonii* Engl., *D. longispatha* Engl. & K. Krause, *D. parvifolia* Engl., and *D. pittieri* Engl. & K. Krause.

MODERN WORK

Very little work was done with *Dieffenbachia* after Engler (1915). Gleason (1929) described *D. pal-*

Table 3. Treatment of *Dieffenbachia* species by A. Engler (1915).

Species treated by A. Engler (1915)	Origin	As treated in this manuscript
1. *D. aglaonematifolia* Engl.	Paraguay	
2. *D. antioquensis* Linden & André	Colombia	
3. *D. aurantiaca* Engl.	Costa Rica	*D. aurantiaca* Engl.
4. *D. bowmannii* Carr.	Colombia & Brazil	
5. *D. brittonii* Engl.	Colombia	
6. *D. cannifolia* Engl.	Peru	
7. *D. cordata* Engl.	Peru	
8. *D. costata* Klotzsch	Colombia & Peru	
9. *D. daguensis* Engl.	Colombia	
10. *D. enderi* Engl.	Colombia	
11. *D. gracilis* Huber	Peru	
12. *D. humilis* Poepp.	Brazil & Peru	
13. *D. imperialis* Linden & André	Peru	
14. *D. latimaculata* Linden & André	Colombia	
15. *D. leopoldii* Bull	Costa Rica	
16. *D. longispatha* Engl. & K. Krause	Panama	*D. longispatha* Engl. & K. Krause
17. *D. macrophylla* Poepp.	Peru	
18. *D. obliqua* Poepp.	Peru	
19. *D. oerstedii* Schott	Central America	*D. oerstedii* Schott
20. *D. olbia* J. Linden & Rodigas	Peru	
21. *D. parlatorei* Linden & André	Colombia	
D. parlatorei var. *marmorea* Linden & André	Unknown	
22. *D. parvifolia* Engl.	Brazil	
23. *D. picta* (Lodd.) Schott	Brazil?	*D. seguine* (Jacq.) Schott
D. picta var. *angustior* Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *angustior* subvar. *angustifolia* Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *angustior* subvar. *jenmanii* (Veitch) Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *angustior* subvar. *lancifolia* (Linden & André) Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *angustior* subvar. *schuttlesworthiana* (Hort. Bull.) Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *barraquiniana* (Verschaff. & Lem.) Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *latior* Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *latior* subvar. *amoena* Hort. Bull.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *latior* subvar. *carderi* Hort. Bull.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *latior* subvar. *gigantea* (Verschaff.) Engl.	Brazil	*D. seguine* (Jacq.) Schott
D. picta var. *latior* subvar. *magnifica* (Linden & Rodigas) Engl.	Venezuela	*D. seguine* (Jacq.) Schott
D. picta var. *latior* subvar. *meleagris* (Linden & Rodigas) Engl.	Ecuador	*D. meleagris* L. Linden & Rodigas
D. picta var. *memoria* (Corsi Salviati) Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. picta var. *latior* subvar. *mirabilis* (Verschaff.) Engl.	Unknown	*D. sequine* (Jacq.) Schott
D. picta var. *latior* subvar. *picturata* (Linden & Rodigas) Engl.	Venezuela	*D. seguine* (Jacq.) Schott
D. picta var. *typica* Engl.	Unknown	*D. seguine* (Jacq.) Schott
24. *D. pittieri* Engl. & K. Krause	Panama	*D. pittieri* Engl. & K. Krause
25. *D. seguine* (L.) Schott	Martinique	*D. seguine* (Jacq.) Schott
= *D. seguine* (Jacq.) Schott		
D. seguine var. *decora* (Hort. Vershaff.) Engl.	Brazil?	*D. seguine* (Jacq.) Schott
D. seguine var. *lineata* (K. Koch & Bouché) Engl.	Venezuela	*D. seguine* (Jacq.) Schott

Table 3. Continued.

Species treated by A. Engler (1915)	Origin	As treated in this manuscript
D. seguine var. *lingulata* (Martius) Engl.	Suriname & Brazil	*D. seguine* (Jacq.) Schott
D. seguine var. *lingulata* subvar. *irrorata* (Mart.) Engl.	Brazil	*D. seguine* (Jacq.) Schott
D. seguine var. *liturata* (Schott) Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. seguine var. *liturata* subvar. *wallisii* (Linden) Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. seguine var. *nobilis* (Hort. Verschaff.) Engl.	Brazil	*D. seguine* (Jacq.) Schott
D. seguine var. *robusta* (K. Koch) Engl.	Unknown	*D. seguine* (Jacq.) Schott
D. seguine var. *ventenatiana* (Schott) Engl.	Suriname	*D. seguine* (Jacq.) Schott
D. seguine var. *viridis* Engl.	Widespread in West Indies, Central and South America	*D. seguine* (Jacq.) Schott
26. *D. weberbaueri* Engl.	Peru	
27. *D. weirii* Berkl.	Colombia	

udicola N. E. Br. ex Gleason from Guayana, and Jonker and Jonker (1966) described *D. elegans* A. M. E. Jonker & Jonker for Suriname. Three species were described from Venezuela, *D. bolivarana* G. S. Bunting (Bunting, 1963), *D. liesneri* Croat, and *D. longipistila* Croat (Croat & Lambert, 1987). Another Venezuelan species, *D. duidae* (Steyerm.) G. S. Bunting, was transferred (Bunting, 1988) from *Spathicarpa duidae* Steyerm., described in 1951.

Dieffenbachia has been so confusing that floristic accounts dealing with Central America have been of little value. Hemsley (1885) listed only a single species, *D. oerstedii* Schott, for his *Biologia Centrali-Americana.* Engler (1915) reported only five species for Central America, *D. oerstedii, D. aurantiaca* Engl., *D. pittieri, D. longispatha, D. seguine,* and *D. leopoldii* Bull. The first four were properly circumscribed, largely owing to the fact that he was dealing with little beyond the type specimens. *Dieffenbachia leopoldii* has proven to be a species known only from Colombia. The only plants Engler (1915) called *D. seguine* were from El Salvador, the type country of *D. wendlandii,* which he erroneously synonymized with *D. seguine. Dieffenbachia wendlandii* differs from *D. seguine* in having unilocular ovaries, and a long-tapered spadix that does not protrude forward at anthesis, as is the case with *D. seguine.*

Matuda (1954) reported only *D. seguine* for Mexico, whereas Bunting (1965) reported both *D. seguine* and *D. oerstedii* for Mexico, the latter being a new report. One of the species that Bunting was dealing with, which he named as *D. seguine,* is recognized herein as *D. wendlandii.*

These earlier floristic accounts for Central America, in addition to being inaccurate, also grossly undercounted the number of existing species. This inaccuracy was in part due to a poor understanding of the collections that existed at the time, but also to the fact that most collections of Araceae have been made in the last 25 years. Panama, for example, has shown vast increases in the number of species collected and identified since the treatment of Araceae in the *Flora of Panama.* Some genera have increased by nearly 544% since 1944 (Croat, 1985). *Dieffenbachia* now has 26 species recognized for Central America, with 77% of them new to science since work on the revision began. This represents a 400% increase from the number reported in Central America by previous workers (Engler, 1915; Standley, 1937, 1944; Standley & Steyermark, 1958; Matuda, 1954; Bunting, 1965).

Standley's treatment of the Araceae of the Lancetilla Valley (Standley, 1931) dealt with only 2 species, *D. oerstedii,* which was at least in part correctly determined, and *D. seguine,* probably *D. standleyi* Croat in the present treatment. However, in the case of the latter species he did not mention the almost fully sheathed petiole that is so distinctive on *D. standleyi.* Standley also confused *D. seguine* with other species, mentioning that it ranged to El Salvador (probably *D. wendlandii*) and to the West Indies (referring to the real *D. seguine*).

The treatment of the Araceae in the *Flora of Guatemala* (Standley & Steyermark, 1958) is especially confusing. In this treatment they dealt with four names, *D. oerstedii, D. picta* (Lodd.) Schott, a maculate species that I consider synonymous with *D. seguine* and not occurring in Central America, and *D. pittieri,* which I consider to be a narrow endemic in the Canal Zone of Panama. Since they did not cite specimens, it is difficult to interpret their treatment, but their description of *D. pittieri* with a petiole sheathed almost to the apex and

ranging from Guatemala to Honduras may be what I am currently calling *D. standleyi*. The plant they were calling *D. oerstedii* probably was, at least in part, the species named. The plant they called *D. seguine* was probably *D. wendlandii*. The mottled plants they referred to as *D. picta* may have been cultivated forms of *D. seguine*, the mottled forms of which are popular with horticulturists and have been known to persist in areas of abandoned dwellings.

The *Flora of Costa Rica* (Standley, 1937) treatment of *Dieffenbachia* was somewhat less confused, probably because it was adapted from Engler's (1911) treatment. Because several of the species types came from Costa Rica, fewer names were misapplied. Here Standley treated *D. aurantiaca*, an endemic to southwestern Costa Rica, *D. leopoldii* (a Colombian species not believed to be in Central America and perhaps confused with what I am calling *D. killipii* in the present treatment), *D. pittieri*, and *D. seguine*. Unfortunately, he cited no specimens nor gave any characters by which to recognize the species. Certainly, no material currently exists in Costa Rica of *D. pittieri* or *D. seguine*.

In the *Flora of Panama*, Standley (1944) did cite specimens for four species. *Dieffenbachia pittieri* is endemic to the Isthmus of Panama. Standley (1944) cited the type, *Pittier 3766*, but he also cited material from El Valle (*Alston & Allen 1839*) that represents *D. crebripistillata*. *Dieffenbachia aurantiaca* was even more confused, with only one of the cited collections, *Woodson & Schery 861*, being *D. aurantiaca*. Other collections cited assign to three different species, *D. isthmia*, *D. killipii*, and *D. tonduzii*. A total of five species were represented among the 12 collections cited as *D. oerstedii*, only one of which actually was that species (*Pittier 2836* in western Panama). Other specimens cited under this name belong to *D. isthmia*, *D. killipii*, *D. nitidipetiolata*, and *D. obscurinervia*.

Collecting History of *Dieffenbachia*

Collecting Araceae has not been particularly popular, and this would be especially true for *Dieffenbachia*. Many collectors who have been careless when collecting *Dieffenbachia* found themselves badly burned with the often high concentrations of oxalic acid in the cut parts. Perhaps this has led to the generally low numbers of collections of *Dieffenbachia*. A survey of those who collected in Central America, based on the extensive TROPICOS database of collections, shows that aside from myself (338 Croat collections for Central America out of a total of 537 Croat collections in the Neotropics) relatively few botanists made many collections of Araceae. Mike Grayum, also an aroid specialist, made 68 collections of *Dieffenbachia* in Central America, mostly Costa Rica, out of a total of 73 *Dieffenbachia* collections for that country. Barry Hammel, a close associate of Grayum and myself, made 57 collections of *Dieffenbachia* in Central America. Paul Standley, one of the most ambitious collectors in the Neotropics made 54 collections. Julian Steyermark, another giant in the field of collecting, made 46 collections, but only 13 of these were in Central America (Guatemala), whereas the balance were from Venezuela. Al Gentry also collected a lot of *Dieffenbachia*, 57 in all, but even fewer were from Central America (only 5 collections).

The earliest botanist to collect Central American species of *Dieffenbachia* was Friedrich Carl Lehmann over a century ago. These were *D. killipii* (*Lehmann 5311*) and *D. tonduzii* (*Lehmann 8876*), the latter as early as 1819. Herman Wendland collected *D. wendlandii*, in this case before 1858. Other collectors included Adolfe Tonduz (*D. aurantiaca*) and Henri Pittier, the first to collect *D. longispatha* (*Pittier 2715*), *D. obscurinervia* (*Pittier 3766*), *D. pittieri* (*Pittier 3766*), and *D. killipii* (*Pittier 2600*), all collected as early as 1911; Paul Standley, who was the first to collect *D. concinna* (*Standley 36739*), *D. isthmia* (*Standley 29867*), and *D. beechiana* (*Standley 36840*), all in 1924; Paul Allen initially collected *D. crebripistillata* (*Allen 1839*) in 1939; E. P. Killip, *D. nitidipetiolata* (*Killip 35113*) in 1939; and Louis O. Williams, *D. horichii* (*Williams 28479*) in 1965.

Other Central American species were collected only in the past few decades. *Dieffenbachia burgeri* dates to William Burger and Ronald Liesner (*Burger & Liesner 7254*) in 1970, and *D. davidsei* was not seen until Scott Mori made his collection in 1974 (*Mori et al. 4184*). Tom Croat encountered *Dieffenbachia fortunensis* in 1976 (*Croat 37268*), *D. galdamesiae* in 1979 (*Croat 49124*), and *D. panamensis* in 1974 (*Croat 27206*). *Dieffenbachia grayumiana* was first noticed by Burger and Matta in 1967 (*Burger & Matta 4181*), *D. fosteri* by Robin Foster in 1993 (*Foster et al. 14649*), and *D. hammelii* by David Neill in 1978 (*Neill & Vincelli 3484*).

Suprageneric Classification of Subfamily Philodendroideae and Relationships of *Dieffenbachia*

Engler (1915) placed *Dieffenbachia* in the subfamily Philodendroideae Engl. The same position is

taken by Bogner and Nicolson (1991) in their modern revision. Grayum (1984, 1990) placed *Dieffenbachia* in its own tribe and does not disagree with Bogner and Nicolson about its relative placement or taxonomic status. However, Grayum substantially modified the Philodendroideae by including the genus *Calla* and thus mandated a change in the name of the subfamily to Calloideae Endl. on the basis of priority. This group, as defined by Grayum, is substantially larger than that of Bogner and Nicolson's, with 40 genera arranged in 17 tribes in five alliances. This contrasts with 18 genera in 7 tribes according to Bogner and Nicolson. The latter system closely mirrors Engler's Philodendroideae, except for the inclusion of new genera and the synonymizing of others since the time of Engler. The size of Grayum's Philodendroideae resulted from the inclusion of tribes from the subfamilies Aroideae Adans., Pothoideae Engl., and Lasioideae Engl. (Croat, 1990 [1992]).

In recent suprageneric classifications by Mayo et al. (1997, 1998) all the genera with unisexual flowers were grouped together in the subfamily Aroideae and further divided into non-ranked groups, the perigoniate Aroideae and aperigoniate Aroideae. *Dieffenbachia*, in the latter group, was placed in the Dieffenbachia alliance, one of four alliances (the others called Philodendron, Schismatoglottis, and Caladium alliances respectively). These alliances comprise 33 genera with an additional 37 genera being placed in a group labeled "No alliance." The classification by Mayo et al. was able to make use of the results of the recently completed chloroplast DNA studies and anatomical studies of French and colleagues (1995, 1997). *Dieffenbachia*, along with *Bognera*, was placed in the tribe Dieffenbachieae, a tribe characterized by having the pistillate flowers completely adnate to the spathe.

In the most recent suprageneric classification of the family by Keating (2002, 2003a) *Dieffenbachia* is included in subfamily Philodendroideae, tribe Spathicarpeae Schott, along with *Bognera*, *Spathantheum* Schott, *Gorgonidium* Schott, *Synandrospadix* Engl., *Gearum* N. E. Br., *Spathicarpa* Hook., *Asterostigma* Fisch. & C. A. Mey., *Mangonia* Schott, and *Taccarum* Brongn. ex Schott. Keating's revision makes use of a wealth of vegetative anatomical information he has accumulated on the family. All members of the Spathicarpeae share in common Type B collenchyma; vascular bundle type II (or occasionally types I or III); and either lack laticifers or have non-anastomosing type laticifers.

The Dieffenbachia alliance of Mayo et al. (1997) is distinguished by having simple laticifers and free synandria. It contains two tribes, the Dieffenbachieae with two genera (*Dieffenbachia* and *Bognera*) and the tribe Spathicarpeae with eight genera, *Mangonia*, *Taccarum*, *Asterostigma*, *Gorgonidium*, *Synandrospadix*, *Gearum*, *Spathantheum*, and *Spathicarpa*. Their tribe Spathicarpeae differs from the tribe Dieffenbachieae in having tuberous stems and leaves with reticulate higher-order venation. However, the latter character is also present in *Bognera*, one of the two genera in their tribe Dieffenbachieae. In the Dieffenbachia alliance Dieffenbachieae are distinguished from other tribes by having anatropous ovules; the primary lateral veins forming a single marginal vein but also lacking collective veins; and, perhaps most importantly, in having the pistillate portion of the spadix completely fused to the spathe. Tribe Dieffenbachieae sensu Mayo et al. (1997) is distinguished from other tribes of subfamily Philodendroideae by having stamens connate into synandria, and in having several free staminodia associated with the female flowers. Other useful distinguishing features include a constricted spathe partly adnate with the pistillate spadix, terrestrial caulescent habit, closely parallel primary and minor veins, and seeds with endosperm.

The Dieffenbachia alliance of Mayo et al. (1997) has been supported by molecular studies with chloroplast *trn*L-F genes (Barabé; Tam et al., 2004). This study shows close relationships between Spathicarpeae and Dieffenbachieae with *Dieffenbachia* being paired with *Spathicarpa* on one branch and with *Cercestis* Schott, *Rhektophyllum* N. E. Br., and *Culcasia* P. Beauv. forming another branch of the tree.

Although both Grayum (1984, 1990) and Bogner and Nicolson (1991) placed *Dieffenbachia* in its own tribe, the authors of both systems now agree that *Bognera*, another Neotropical genus, is very close to or within the tribe Dieffenbachieae, sensu Mayo et al. (1997). Keating (2002, 2003a) simply subsumed this tribe (or its genera) within his larger Spathicarpeae, still in essential agreement.

The subfamily Philodendroideae is worldwide in distribution and, sensu Grayum (pers. comm.), it is somewhat equally divided between the Old World and the New World, with 19 genera (17 of them endemic) and 761 species in the New World and 23 (21 endemic) genera and 354 species in the Old World. Grayum places the Dieffenbachieae in his Aglaonema alliance with Zantedeschieae Engl. (*Zantedeschia* Spreng.), Aglaonemateae Engl. (*Aglaonema* Schott, *Aglaodorum* Schott), Spathicarpeae (*Mangonia*, *Asterostigma*, *Synandrospadix*, *Taccarum*, *Gorgonidium*, *Gearum*, *Spathanthemum*, *Spathicarpa*), and Bognereae S. Mayo & D. Nicol-

son (*Bognera*). Anubiadeae Engl. (1876) (*Anubias* Schott) and Zantedeschieae are restricted to Africa, while the Spathicarpeae are restricted to southern South America.

Morphology of Vegetative Structures

habit and growth patterns

Dieffenbachia is always terrestrial and caulescent (Croat, 1988 [1990]). In terms of growth behavior and habit, *Dieffenbachia* is not as variable as *Philodendron*, a related genus, but sterile plants disassociated with notes about habit can be confused with those of *Philodendron*. Stems of *Dieffenbachia* are erect, at least on the younger portions, with older portions of the stem typically becoming decumbent. This creeping portion of the stem is sometimes even longer than the erect portion (Fig. 23A). The overall height of any species is usually determined by the thickness, strength, and rigidity of the stem. Typically, species such as *D. burgeri*, *D. hammelii*, and most plants of *D. oerstedii*, with small-diameter stems, do not get to more than 1 m tall nor do they usually have stems more than 2.5 cm in diameter. Alternatively, the taller species like *D. horichii*, *D. longispatha*, and *D. standleyi* have thick stems and reach heights of 2 to 3.5 m. Cultivated plants growing in a pot and unable to become reclined at the base can grow to indefinite height. A plant of *D. standleyi* cultivated in the greenhouse of the Missouri Botanical Garden grew up the side of a wall from a pot to the height of 8 m.

The portion of the stem that comes in contact with the ground becomes rooted at the nodes, but stems are rarely buried. Instead, the stems usually creep over the surface of the ground. The growth behavior often leads to vegetative reproduction, since on some species the creeping portion of the stem tends to produce active branch buds that form new growth. Another feature that tends to induce additional branching is the often fragile stem extending laterally over the ground, which may be broken by being walked on by animals. Broken stems invariably produce new branches. These results often cause *Dieffenbachia* to grow in large colonies, especially in open, better illuminated areas of the understory of a forest, along stream banks or in open swamps. Examples of colonial growth occur in *D. crebripistillata*, *D. isthmia*, *D. killipii*, and *D. oerstedii*. Some species, such as the taller *D. longispatha* (to 3.5 m), are usually less colonial. This is perhaps because it is a species with a large, stout stem that is less likely to be broken up by the elements. This species also has a thicker sap that is more foul-scented and caustic than many other species, and may in part account for less breakage by deterring animals from the plant.

In some cases *Dieffenbachia* may grow in standing water. In such cases the stems may be rather deeply buried in the mud. Some species, such as *D. grayumiana*, are frequent in wet habitats, but most species thrive in well-drained soils. The genus is seldom found on road embankments, a habitat that is very common for species of *Anthurium* and *Philodendron*. This is perhaps because the two latter, principally hemi-epiphytic genera can more easily become established on the excessively well-drained and poor clay soils of typical road embankments in the Neotropics.

Development in *Dieffenbachia* is never heteroblastic. Instead, changes in internode size and leaf size progress without any marked changes in blade shape. However, leaf blades of *Dieffenbachia* that ultimately become cordate at the base are at first simple and acute to obtuse at the base.

stems

Internodes are typically about as long as broad or even shorter than broad. Sometimes, as in the case of *D. galdamesiae*, petioles are affixed to the stem at an oblique angle and the internodes are not of equal width across the diameter of the stem. Instead, one side is as much as 1 cm wider than the other. Most commonly, internodes are glossy to semiglossy and smooth, though they may be minutely roughened, appearing with a somewhat weak velvety sheen, as in the case of *D. oerstedii*. Though for most species the internodes remain moderately glossy even in age, when fresh, the internodes may change promptly. In *D. obscurinervia*, the stem, though initially semiglossy, promptly becomes etched in a deep, areolate pattern to such an extent that the stem becomes matte and is conspicuously scurfy.

Cataphylls are never present on *Dieffenbachia*. Instead, the new growth on stems of *Dieffenbachia* is protected by the sheathing petiole of the preceding leaf.

Stem color varies considerably between species and even within populations of the same species. Species such as *D. longispatha*, which typically possess stems that are solid green, can sometimes be variegated with paler colors. Typically, stem color variegation is in the form of streaks rather than mottling. The stem may be relatively dark green with even darker streaks, in which case the mottling would not be too apparent, or, as is more frequently the case, it may be streaked with pale

green or yellow-green. Dried stems are often highly diagnostic for key characters such as the degree to which they are contorted, usually ridged or cracked, or the color that they dry.

LEAVES

Leaves may be clustered near the apex of the stem such as in *Dieffenbachia panamensis* or sometimes they are rather well scattered along the stem as in *D. grayumiana.*

Dieffenbachia petioles are on average shorter than the blades, ranging from 0.23 to 1.08 as long as blades, and averaging 0.65 times as long as blades. Typically, the blades average about 1.5 times longer than the petioles. The petioles are typically sheathed for a significant portion of their length. The extent and nature of the leaf sheath constitutes one of the most important species-level characters. The sheath margins are virtually always persistent, but the degree to which the sheath is open, i.e., erect-spreading (Fig. 24D), erect, or inrolled, remains an important characteristic. The petiole sheaths of *D. wendlandii* are typically inrolled at the apex, whereas the sheath of *D. oerstedii* is erect. The petiole sheath is typically unequal at the apex with one side more acute than the other. Some species (*D. davidsei, D. seguine*) have the petiole sheath free-ending (Figs. 8D, 23D).

Petiole cross-sectional shape is given only for the free portion of the petiole (when present). While sometimes variable within the species, it often constitutes an important taxonomic difference between species. Petioles are most commonly subterete with the adaxial surface frequently somewhat flattened (as in *D. longispatha,* Fig. 16C) or sulcate (*D. beachiana,* Fig. 3D). When sulcate the petioles may be obtusely sulcate or sharply sulcate, as is usually the case in *D. oerstedii* (Fig. 20D). Though rare, the petiole cross-sectional shape may be triangular, as in *D. aurantiaca* where, in addition to being flattened adaxially, the lateral margins are bluntly winged and spreading (Fig. 2C, D). In *D. panamensis* the free portion of the petiole is also winged; the wing itself is usually thin, spreading, and markedly undulate. The free portion of the petiole may also have a prominently winged margin with the wing itself usually thin and undulating as in *D. panamensis* and *D. standleyi* (Fig. 24).

Dieffenbachia has leaf blades usually considerably longer than the petioles, ranging from 0.9 to 4.3 times longer than the petioles. Blades are typically conspicuously longer than wide, ranging from 1.1 to 4.3 times longer than wide. The blades are similar to those of many species of *Philodendron,* and sterile specimens for which habit is not mentioned are often difficult to separate from *Philodendron.* Most leaf blades are ovate to oblong-ovate, elliptic, oblanceolate or obovate, and are usually acuminate at the apex and acute to obtuse or rounded at the base (rarely subcordate at base as in *D. wendlandii* and *D. isthmia*). As is true of *Philodendron, Dieffenbachia* vernation is always supervolute (Cullen, 1978).

Venation patterns are similar to those in *Philodendron* (cf. Croat, 1997). The midrib is especially variable and diagnostic, especially on the adaxial surface, being usually prominently raised and varying from angular to broadly convex. The shape of the midrib is often taxonomically significant. In *D. killipii* the upper midrib is raised with square margins (Fig. 15B, C). In other cases the midrib may be broadly convex as in *D. panamensis* (Fig. 21D) or flat to sulcate as in *D. standleyi.* The midrib color is also important, since the midrib may be conspicuously paler than the lamina as sometimes in *D. oerstedii* (Fig. 20) or concolorous as in *D. galdamesiae* (Fig. 10B). In *D. obscurinervia* the midrib may be conspicuously speckled as is the petiole (Fig. 19C).

Primary lateral veins are usually well spaced with many, much finer minor veins between each pair of primary lateral veins. In all cases, the primary lateral veins extend to the margin and do not form a collective vein that extends all the way to the apex. Instead the primary lateral veins typically course along the margin of the blade, where they may form a weak collective vein that joins several primary lateral veins (especially near the middle of the blade) that eventually merge with the margin before reaching the apex. Primary lateral veins are usually somewhat sunken to weakly quilted-sunken above and raised on the lower surface (sometimes thicker than broad and sometimes weakly pleated-raised). Blades of *D. davidsei* may be rather conspicuously quilted-sunken (Fig. 8B). Leaf blades typically are glabrous, but the major veins may rarely be puberulent, as in *D. beachiana,* to granular-puberulent or conspicuously granular, as in *D. fortunensis* (Fig. 9C). Minor veins may arise only from the midrib, as appears to be the case in *D. longispatha* and *D. nitidipetiolata,* or they may arise from both the midrib and the primary lateral veins. The latter situation appears to be the most common in *Dieffenbachia.*

MORPHOLOGY OF FLOWERING STRUCTURES

INFLORESCENCES

Dieffenbachia inflorescences are far less diagnostic than those of *Philodendron,* since nearly all

are solid green on both surfaces. There are considerable differences in the number of inflorescences per axil, ranging from solitary on a number of species at least part of the time or up to eight per axil as with *D. concinna*. In any population the number of inflorescences per axil may vary. Studies made with *D. oerstedii* in Costa Rica (Valerio, 1984) showed that this species produced primarily one or two inflorescences per axil.

SPATHE

Each spathe in a cluster of inflorescences in *Dieffenbachia* is subtended by linear-lanceolate bracteoles, each of which are unribbed. The bracteoles are typically about as long as the peduncles, but can sometimes be shorter or longer. They are somewhat marcescent.

Spathes of *Dieffenbachia* are uniformly green, though the inner surface tends to be somewhat paler than the outer surface and frequently much glossier. The outer spathe surface is typically semiglossy to weakly glossy. Sometimes the inner surface of the spathe is somewhat whitish on the inside near the tip.

The spathe of most *Dieffenbachia* is only weakly constricted above the spathe tube (Figs. 7A, 16D, 20F, 22E, 23E, 24F, 25F). When the entire spathe is fully flattened, the tube portion is considerably wider (Figs. 2B, 15H, 22F, 23F) and the spathe is gradually tapered from the lower ¼ to the usually acuminate apex (Fig. 23F). Sometimes there is a weak central constriction. The point of maximum constriction corresponds to the sterile section of the spadix between the fertile staminate flowers and the pistillate flowers.

At anthesis the spathe of *Dieffenbachia* is open to about the middle (Figs. 5B, 7A, 13E, 16D), or somewhat below the middle, but does not open as widely as that of *Philodendron*. At anthesis the spathe blade is wider than the tube. Typically only the staminate portion of the spadix is visible at anthesis but sometimes, as in *D. crebripistillata*, a portion of the pistillate spadix is also exposed. Closure of the spathe after anthesis is sometimes not complete, with the margins of the spathe meeting irregularly. At anthesis the blade of the spathe is usually arched somewhat forward, hooding the spadix slightly. For some species, such as *D. crebripistillata*, the spathe may be recurled at anthesis (Fig. 7C).

SPADIX

Flowers of *Dieffenbachia* are unisexual and naked, dispersed on the spadix in the typical manner with the staminate flowers at the apex and the pistillate flowers at the base. The spadix of *Dieffenbachia* is usually shorter than the spathe by 1–3 cm (Fig. 2B). The spadix is contained within the spathe, and is more or less straight or weakly curved (Fig. 8F) at anthesis, rather than being prominently protruded forward. Some species have the spadix protruded forward at anthesis, such as *D. burgeri* (Fig. 4C), *D. crebripistillata* (Fig. 7C), *D. horichii* (Fig. 13E), *D. wendlandii* (Fig. 26C), and *D. seguine* (Fig. 23E). The last species, which ranges throughout the West Indies, has a spadix that notably protrudes and is cylindrical, rather than tapered to the apex as in the remaining Central American species (Fig. 23F). *Dieffenbachia seguine* also has a spadix (Fig. 23) that is caught in the protruded position when the spathe re-closes. In contrast to *D. seguine*, all of the Central American species have spathes that close normally with the spadix withdrawing inside of the spathe.

Like other members of the Philodendroideae, the spadix in *Dieffenbachia* is divided up into a fertile staminate section at the apex, a sterile section lying beneath the fertile staminate portion, and the pistillate portion (Figs. 2B, 7, 18, 25). The lowermost section, as with all Araceae with unisexual flowers, is the pistillate section. Typically the pistillate portion and the staminate portion are of roughly equal lengths, but the length of the sterile segment (when apparent) is highly variable both in terms of length and the degree to which staminodia and pistillodes are dispersed on it (Figs. 2B, 4C, 5D, 7, 15H, 18D, 23F, 25G). In most cases the pistillate region is slightly longer than the staminate.

The fertile staminate portion is somewhat cylindroid to spindle-shaped, broadest in the middle and weakly tapered toward both ends, being bluntly rounded at the apex. The fertile male flowers are compacted and sub-rounded or with angular margins (Figs. 2E, 5G). As the spadix approaches anthesis the synandria loosen and the anthers become visible between the synandria. Toward the base of the staminate portion of the spadix, the flowers are somewhat more irregular in size and shape, but do not become radically different as in the case of *Philodendron* and *Xanthosoma*, where the lowermost male flowers are sterile and swollen. In contrast, *Dieffenbachia* relies entirely on club-shaped staminodia surrounding the pistils (Figs. 5E, 14C). The lowermost staminate flowers are smaller or very irregular in shape, sometimes showing signs of two or more flowers fused together. Sometimes the uppermost pistils are reduced, apparently sterile, and surrounded by sterile male flowers (Fig. 15H). Apparently the lowermost staminate flowers are also

more attractive to beetle pollinators, since only the lowermost flowers are eaten (Fig. 1B).

ANDROECIUM

Staminate flowers consist of 4 stamens united into a 4- or 5-sulcate truncate synandrium (Figs. 2E, 5G, 23G, 26E). The apex of the synandrium often has a minute slit or an equidistant series of 3 minute slits connected at the center. Upon drying the apex of the synandrium may become wrinkled along the margin and may also have a concave surface. The anthers are contiguous or nearly so, affixed near the upper edge of the synandrium. The thecae are obovoid to cylindroid, opening by apical slits just below the upper edge of the synandrium. The pollen is dispersed in slender, subterete filaments and typically projects up to 1 cm above the surface of the synandrium. When the stamens are at anthesis, the shedding pollen can completely fill the now closing spathe (Fig. 5F).

POLLEN

Pollen of *Dieffenbachia* is released in monads that are inaperturate, subisopolar to virtually polar, boat-shaped-elliptic to oblong, or nearly spherical. They are bilaterally symmetrical or radiosymmetric (Grayum, 1992).

Dieffenbachia pollen is moderately large for Araceae, ranging from 54 to 99 μm (as in *D. oerstedii*) and averaging 79 μm. Exine sculpturing is psilate to obscurely verruculate (as in *D. oerstedii*) and/or sparingly punctate-foveate to densely foveate with scattered compound foveolae (as in *D. pittieri* and *D. seguine*). Grayum (1992) pointed out that the compound foveolae found on the pollen of *D. pittieri* and *D. seguine* resemble those of *Chlorospatha croatiana* Grayum.

STERILE SPADIX SECTION

Dieffenbachia typically has a nearly barren section of the spadix lying between the fertile staminate portion at the apex and the pistillate portion at the base (Figs. 5D, 23F). This section occurs in the area where the spadix first becomes free from the spathe. Only rarely is the transition between the fertile staminate and the sterile portion of the spadix clearly defined with the fertile flowers abruptly ending on a clear flowerless sterile portion. Instead, there is usually an assortment of sterile male flowers toward the apex of the sterile segment (Fig. 7E). Less frequently there are pistillodes in the lower half of the sterile segment. In *D. beachiana* and *D. killipii* (Fig. 15H) the sterile section is apparently absent, with the fertile staminate and fertile pistillate portions essentially contiguous. The length of the sterile portion of the spadix is here defined as that portion which lies between the lowermost functional androecium and the uppermost functional pistil regardless of the presence of pistillodes and staminodes along its length. However, the sterile portion of the spadix is usually quite obvious since a significant proportion of the sterile section is devoid of flowers. The axis of the sterile portion is typically convex as if the terete axis of the spadix (now fused) was half sunken into the leafy tissue of the spathe.

PISTILLATE SPADIX

The pistillate portion of the spadix is fused throughout its entire length to the spathe. What appears to be a stipe is readily apparent at the base. The pistillate flowers rarely extend very close to the base of the spathe (Fig. 4C). After the presence or absence of a sterile segment in the spadix, the number and disposition of the pistils is perhaps the most important taxonomic character in the inflorescence. Unlike many genera in the Philodendroideae that have the pistillate flowers closely aggregated on the spadix, the pistillate flowers of *Dieffenbachia* are moderately dispersed on the spadix. The degree of dispersal on the spadix is in itself different from species to species. There are generally only 2 or 3 pistils across the width of the spadix axis (regardless of whether they are lined up or not). Rarely, as in the case of *D. killipii*, there up to 6 pistils visible across the width of the spadix. At the opposite extreme, *D. longispatha* sometimes has a solitary row of pistils across the spadix axis. The arrangement of the pistils is generally quite irregular, lacking any obvious equidistant spacing or alignment in rows, but sometimes a series of pistils might be arranged in a loose row (as in *D. killipii*) or even in a broad arc across the width of the spadix.

Pistils are 2- or 3-carpellate, sometimes 1-carpellate, sessile, depressed-globose to depressed-ovoid, pale green, semiglossy, and smooth or 2- or 3-lobate. The stigma is a 2- or 3-lobate cushion-like layer that covers the entire apex of the pistil. The stigmatic papillae are orange or yellow. The papillae are close, dense, and moderately short, similar to those of *Philodendron*, but appear less interspersed with the gelatinous matrix that is so common on the stigmas of that genus. The stylar region is inconspicuous. With the stigma removed, the surface is truncate or broadly sulcate with a solitary medial or near-medial pore. Ovules are

anatropous, one per locule. Each pistil is surrounded by 4 or 5 claviform, fleshy, white staminodia. The staminodia may be fused somewhat at the base, often forming a cupuliform structure around the base of the pistil. Individual staminodia are subcylindrical, commonly somewhat flattened toward the base and usually enlarged, sometimes almost subglobular at the apex. Staminodia typically are erect-spreading or erect, vary considerably in length, but are almost invariably longer than the pistils, usually 2–5 mm long, and held well above the pistils.

Morphology of Fruiting Structures

infructescence and fruit

While the inflorescences are always first erect, they quickly become reflexed after anthesis. This is probably important to successful development of the infructescence as it prevents the spathe from filling with rainwater and thus possible decay.

Fruits develop within the re-closed spathe, which often turns yellow, pale to bright orange, or red as fruits begin to mature. The spathe enlarges somewhat during the course of maturation, and finally begins to reflex along the middle, especially the portion that is fused to the spadix. In the process most of the margins of the spathe slough off, leaving just the fruiting spadix. The spadix remains arched backward with the bright red to orange-red berries held somewhat apart by the recurving process and displayed against the generally pale remains of the spathe (Figs. 1D, 4D).

Although fruit develops with self pollination, fruit and seed size are greater when the plants are out-crossed (Young, 1986). Since *Dieffenbachia* flowers are naked, all protection of the flowers must be provided by the spathe. In the manner of many other genera in the Philodendroideae, the spathe re-closes over the female flowers after pollination. In most cases, protection of the developing fruits after pollination is provided by the thickness of the spathe, as is true of other aroid genera such as *Philodendron*, but in *Dieffenbachia* protection is also provided by toxins in the sap, which may burn the mouth of any animal eating it. However, the pericarp and mesocarp of the berry appear to have no injurious effects when eaten and apparently lack the same toxic effects found elsewhere.

Generally, most pistils of an inflorescence are pollinated and develop into fruits, but the number produced per plant is variable. Studies in Costa Rica on *D. oerstedii* (Valerio, 1984) showed that the fruits varied from 13 to 43 with an average of 26 per plant. Valerio also reported that some berries were sterile, varying from 1 to 17 per infructescence.

Germination of seeds is usually prompt if the mesocarp is first removed. Valerio (1984) found that naked seeds of cleaned berries of *D. oerstedii* began to germinate within four days in a germination chamber. The percentage of seeds germinating ranged from 77.3% to 100% for different infructescences (averaging 91.7%). However, berries left intact usually did not germinate, but remainded viable for up to 90 days.

Valerio (1984) also reported that although 82% of the 729 berries studied were green, the remainder were red or yellowish. All seeds produced only albino plants. Germination rates for both the green seeds and the abnormal seeds were the same, but the albino plants perished. His studies with seed germination of *D. oerstedii*, as well as observations of other plants in the field led him to conclude that plants of this species required between five and six years to reach reproductive age.

Fruit maturation is normally a slow process in *Dieffenbachia*, requiring up to nine months in the case of *D. nitidipetiolata* (Young, 1986) (reported as *D. longispatha*). Valerio (1984) reported that fruit maturation in *D. oerstedii* was approximately one year. Valerio (1984) suggested that the seeds of *Dieffenbachia* are bird-dispersed because the seeds will not germinate unless the fruit mesocarp is first removed. At maturity the mesocarp of *Dieffenbachia* berries is pasty and somewhat sweet. The fruits would appear to be most suitable to bird dispersal, being colorful and having only a thin layer of edible portion available. The seeds are soft and could easily be destroyed by chewing, so effective animal dispersers are probably just removing the pericarp and thin mesocarp. Fruits of *Dieffenbachia* have been observed being eaten by white-faced monkeys, *Cebus capucinus* (J. Oppenheimer, pers. comm.), but it is not known whether they are the primary dispersal agents, since cebus monkeys are known to be generalists in their eating behavior (J. Oppenheimer, pers. comm.).

flowering behavior and pollination

Dieffenbachia populations tend to be aggregated, perhaps due as much to the vegetative reproduction of the stems as by local germination of seeds. A single clone may have many stems, but relatively few stems flower in a given year, and the number of inflorescences open on a given day is few (Young, 1988b). Inflorescences borne on a single stem generally do not anthesally overlap, thus there is little potential for geitonogamy (Young, 1990). For *D. ni-*

tidipetiolata (reported as *D. longispatha* in Young, 1988b) a reproductive stem may have two to seven inflorescences during a single growing season, maturing at intervals of 3 to 12 days (Young, 1986). For *D. oerstedii* there may be between one and four inflorescences per axil. Valerio (1984) reported that plants which produced a solitary inflorescence (34 of the 83 plants studied produced inflorescences) did not develop fruit. Valerio was unable to ascertain whether this was due to a lack of pollinators or age of the plants.

The pollination biology of *Dieffenbachia* has been studied (Croat, 1978, 1983b; Valerio, 1984; Young, 1986, 1988a, 1990). It has long been known to aroid workers that *Dieffenbachia* and several other aroid genera, e.g., *Philodendron*, some *Syngonium*, and *Xanthosoma*, are visited regularly by large scarab beetles (Coleoptera). Young (1986, 1990) found that *D. nitidipetiolata* (reported as *D. longispatha*) is pollinated mostly by beetles of the genus *Cyclocephala* (Scarabaeideae, Dynastineae) or more infrequently by the genus *Erioscelis*, also a dynastine scarab. Other visitors, including Diptera, Hemiptera, Dermaptera, Thysanoptera, and nitidulid beetles (Coleoptera, Nitudulidae), proved not to carry pollen and were deemed by Young not to be pollinators (Young, 1990).

Other monoecious aroid genera, such as *Philodendron* and *Xanthosoma*, are known to be beetle pollinated and provide food by means of oil-rich sterile male flowers. In *Dieffenbachia* the food reward consists of the protein-rich club-shaped staminodia surrounding each female flower (Young, 1986, 1990), but the beetles have also been seen feeding on the lowermost portion of the fertile staminate portion of the spadix. An indication that the staminodial food source is important to the beetles and preferred over other floral parts, is that the beetles will leave an inflorescence.

The production of scents during flowering is facilitated by the thermogenic behavior of the spadix, which may increase as much as 4°C during anthesis (Young, 1990). Scent production coincides with the flight activity of the scarab beetle pollinators (Schatz, 1990). Active movement of pollinators is usually at dusk, seemingly in direct paths to an open inflorescence. Beetles arrive at the inflorescence by first landing on the spadix (Young, 1990), then entering the lower tube portion of the spathe where the pistillate portion of the spathe is at anthesis. Beetles typically remain in the inflorescence for 24 hr. after their arrival. While in the spathe the beetles mate and eat the nutritious staminodia (Young, 1986) surrounding the pistils. Beetles depart the following day as the inflorescence begins to close and the staminate flowers are emitting pollen in long filaments (Fig. 5F). In order to leave the inflorescence the beetle must literally wade through pollen, ensuring that it will be covered with pollen before flying away to the next receptive inflorescence.

While some *Dieffenbachia* species, perhaps most, have spathes that remain open only 24 hr. (based on my observations in the field), the pollination event for *D. nitidipetiolata* (reported by Young as *D. longispatha*) involves three days (Young, 1990). Inflorescences of this species open in the evening of the first day, but the spadix is not initially receptive. On the evening of the second day the stigmas become receptive (about 17:30) and the spadix temperature increases to 4°C above ambient temperature (Young, 1990). It is at this time that beetle pollinators arrive, and they enter the spathe where they generally persist for another full day, departing on the evening of the third day. Young (1990) found that for most days there were fewer than four inflorescences open and in female phase at any one time in an area of 700,000 m^2. In her studies at La Selva in Costa Rica she found that beetles flew between 1 and 680 m (averaging 83 m) between consecutive visits to *D. nitidipetiolata* (reported as *D. longispatha*).

Beetle pollination of *Dieffenbachia* is not species-specific. Nine different scarab beetle species of *Cyclocephala* as well as *Erioscelis columbica* Endrodi were found to pollinate *D. nitidipetiolata* (reported by Young as *D. longispatha*) at the La Selva Reserve in Costa Rica (Young, 1986). Still, *Dieffenbachia* species produce different scents and differentially attract particular beetle species (G. Schatz, pers. comm.).

Because of the loose relationship between the pollinators and any one species of *Dieffenbachia*, hybridization does occasionally occur (Young, pers. comm.). It is known that seeds from hybrid plants do germinate and produce viable F1 plants. It has not yet been determined if this F1 generation is capable of reproducing sexually. Still, this phenomenon of hybridization might explain the many different, seemingly related, but distinct, populations of *D. nitidipetiolata* that occur in some regions, such as the Río Guanche region of Colón Province in Panama. Since asexual reproduction is so prevalent in *Dieffenbachia*, occasional hybridization followed by vegetative reproduction might explain these patterns of variation.

PHENOLOGY

Some species of *Dieffenbachia* are in flower all year-round. In general, more flowering takes place

during the rainy season even if the species flowers at other times of the year as well. This may be tied to the fact that the beetles pollinating *Dieffenbachia* are more frequent during wet periods. Although *D. beachiana* and *D. burgeri* flower primarily in the dry season in Costa Rica and Panama, they occur in wetter habitats where beetle pollinators are reliably available.

CYTOLOGY

Dieffenbachia has chromosome counts of $2n = 34$ and 68 (Petersen, 1989). Grayum argued that *Dieffenbachia* is closely related to *Philodendron* (Grayum, 1984). Petersen (1989) argued that *Philodendron* would not be considered so closely related if its chromosome base number were not 17 as assumed by Grayum. She also argued that the differences in the "size and constitution of the chromosomes (small metacentrics of *Philodendron* versus medium to large submetacentrics to subtelocentrics of *Dieffenbachia*) also indicate that no close relationship exists between the two genera" (Petersen, 1989: 128). Petersen considered the chromosome basic number in *Philodendron* to be $x = 18$ based on the fact that all members of *Philodendron* subg. *Meconostigma* (Schott) Engl. have $2n = 18$ and subgenus *Philodendron* Schott also has $2n = 18$ in part. Grayum (1984) suggested that *Dieffenbachia* was close to the tribe Spathicarpeae (subfam. Aroideae). Petersen (1989) considered this a reasonable suggestion since they share the same basic number of $x = 17$ and large chromosomes also with the centromere frequently located distally on the chromatids. Petersen (1989) believed that the Aglaonemateae may be the closest relatives of Dieffenbachieae based on the similarity in the constitution and size of the chromosomes, despite the fact that the former has a different chromosome base number ($x = 20$). Chromosome counts for *Bognera recondita* (Madison) Mayo & Nicolson, the only other member of Dieffenbachieae, are also $2n = 34$. *Bognera*, a monotypic genus, also shares a karyotype of medium-sized metacentric to sub-telocentric chromosomes with *Dieffenbachia* (Petersen, 1989).

GEOGRAPHICAL DISTRIBUTION AND ENDEMISM

The genus *Dieffenbachia* has approximately 135 species, most of them in South America. It ranges from Mexico, throughout Central America, and to the West Indies, Trinidad, and most of South America as far south as Argentina, Paraguay, and Bolivia. Distribution of species is unequal, with major centers of diversity including Colombia with 37 species, Ecuador (34), Peru (30), Brazil (27), Panama (20), and Costa Rica (13), principally at lower to middle elevations in the Andes. The genus is also widespread in the Amazon basin as is evidenced by the large number of species at low elevations in Brazil with a total of 27 species. Only 8 species occur in the Guianas region in eastern South America and the Territorio Amapá of northeastern Brazil. The genus is exceptionally abundant in the western Amazon basin in the foothills of the eastern Andes, with 57 species. The wetter forests at middle elevations in the foothills of the Andes are particularly rich. For example, there are 5 species in the vicinity of the Jatún Sacha Reserve along the Upper Río Napo near Misahuallí in Ecuador.

As is true for many other genera of Araceae (Croat, 1992, 1983a, 1986a, 1986b), the northwestern part of South America, especially on the Pacific slope of Colombia and adjacent Ecuador, is rich in species of *Dieffenbachia*. About 14 species occur on the eastern slopes of the Andes in Ecuador and about 15 species are known from the Pacific slope in Colombia. Relatively few species occur in southern South America, with only *Dieffenbachia aglaonematifolia* Engl. occurring in southern Brazil, Paraguay (Croat & Mount, 1988), and Argentina. Collections of only 7 species, mostly new species, have been seen for Bolivia. North-central South America is also not particularly rich in species. Only 2 species occur in the Cordillera de Mérida in Venezuela, and only 1 of these occurs in the Cordillera de la Costa (Bunting, 1979; Croat & Lambert, 1987).

A preliminary key and preliminary descriptions have been produced for South American *Dieffenbachia* species, but many species remain poorly known. Thus the figures given for South America remain tentative.

Central American species constitute a group relatively isolated from South America, and only seven species range into South America, especially along the Pacific slope and in the Magdalena River Valley in Antioquia Department. The majority of *Dieffenbachia* in Central America occur from Nicaragua to Panama, and most are relatively widespread in this region. The most widespread species of *Dieffenbachia*, *D. oerstedii*, ranges from southern Mexico to western Panama (Fig. 29). *Dieffenbachia wendlandii* ranges from Mexico to Costa Rica (Fig. 28) and both *D. nitidipetiolata* and *D. tonduzii* range from southeastern Nicaragua to Ecuador (Figs. 30 & 29, respectively). In the latter country, *D. nitidipetiolata* crosses the Andes into the Amazon drainage in Napo. Remaining *Dieffenbachia* are all narrowly isolated. Nine species are shared between

Costa Rica and Panama, but even these are not widespread in the two countries. Those shared are *D. aurantiaca, D. beachiana, D. davidsei, D. grayumiana, D. killipii, D. nitidipetiolata, D. oerstedii, D. tonduzii,* and *D. wendlandii. Dieffenbachia aurantiaca* occurs only in southwestern Costa Rica in the vicinity of the Osa Peninsula and in adjacent Panama in the Burica Peninsula area (Fig. 27). Both *Dieffenbachia beachiana* and *D. grayumiana* range from northern Costa Rica to western Panama (Bocas del Toro) (Figs. 28, 27), while *D. davidsei* ranges from northwestern Costa Rica to central Panama (San Blas) and Colombia (Fig. 27).

A total of 11 species (42% of the total) of *Dieffenbachia* are endemic to either Costa Rica or Panama. Endemism is particularly high in Panama where 8 of the 26 species (31%) are endemic. In Panama endemic species are *D. copensis, D. crebripistillata, D. fosteri, D. fortunensis, D. galdamesiae, D. lutheri, D. panamensis,* and *D. pittieri* (Figs. 27–30). In Costa Rica 3 of 26 species (12%) are endemic. Costa Rican endemics are *D. burgeri, D. hammelii,* and *D. horichii* (Fig. 27). Neither Mexico nor Middle America have endemic species.

Dieffenbachia isthmia (Fig. 28), *D. longispatha* (Fig. 29), and *D. obscurinervia* (Fig. 29) range across the Isthmus of Panama from Veraguas Province to northern Colombia. *Dieffenbachia aurantiaca, D. beachiana,* and *D. grayumiana* (Figs. 27, 28) are the only species occurring in both Costa Rica and Panama. Some species are further isolated. *Dieffenbachia aurantiaca* and *D. burgeri* are restricted to the region of the Osa Peninsula in southwestern Costa Rica (or in the case of *D. aurantiaca* in Panama on the adjacent Burica Peninsula; Fig. 27) and *D. horichii* is restricted to a relatively small area on the Pacific slope of Costa Rica (Fig. 27). Several other species are also narrowly restricted or known only from the type specimen. *Dieffenbachia fosteri* is restricted to northeastern Panama (Fig. 27). *Dieffenbachia fortunensis* is restricted to the northern Chiriquí Province (Fig. 28). *Dieffenbachia copensis* is found only in the Coclé Province of Panama (Fig. 27), and *D. galdamesiae* in a small area south of the Panama Canal (Fig. 28).

Further collecting in Colombia, especially along the western slope of the Andes, may change the distribution of *Dieffenbachia,* but the current patterns most likely reflect the realities of life zone ecology and geologic history of the area rather than under-collecting. Since relatively few species of Araceae are known to occur at lower elevations on both the eastern and western side of the Andes, it can be presumed that the evolution of the respective Amazonian and Pacific coastal floras occurred independently after the Andes began to arise toward the end of the Cretaceous (Raven & Axelrod, 1974). The fact that there are no truly wide-ranging species, i.e., those ranging from Mexico to Brazil, attests to this isolation. The high rates of endemism in Costa Rica and Panama as well as Mexico perhaps reflects the isolation of these areas during periods when the oceans were at much higher levels than they are today, and when the area that is now central Panama and Costa Rica was subsequently disconnected from South America. At the close of the Tertiary period, 18,000 years ago, the sea level was about 100 m higher than today (Holmes, 1969). Much earlier the land mass of what is now Central America began to emerge as a series of islands during the Oligocene epoch with further uplifting during the Middle Miocene. It was not until the Upper Miocene and Pliocene epochs that the final portions of the isthmus of Panama emerged above sea level (Torre, 1965), and the final connection of Central and South America was about 5.7 million years ago. To put these geological events in relation to the modern aroid flora, it should be noted that even during this era precursors to the extant flora probably already existed. The angiosperm floras of the Oligocene were believed to have consisted almost entirely of extant genera and with existing species among Oligocene and Pliocene floras (Takhtajan, 1969).

Equally important as geology to the isolation of the Central American aroid flora are ecological factors for Central American species of *Dieffenbachia.* Much of eastern Panama consists of broad expanses of *Tropical moist forest* (T-mf) with other, generally smaller areas of *Premontane wet* (P-wf) and *Tropical wet forest* (T-mf) (Holdridge, 1967). In contrast to Panama, much of the Chocó area of northwestern Colombia consists of much wetter pluvial forest with annual precipitation exceeding 11,700 mm (Gentry, 1982). This broad band of pluvial forest with its own suite of unique endemic species no doubt acts as a dispersal barrier for species from regions with less rainfall. It may account for those Panamanian and Costa Rican species that skip the wettest areas of northwestern South America but reoccur in the relatively drier areas of mesic western Ecuador.

Middle America has low species diversity with Guatemala having only two species and Honduras three. Only Nicaragua, with six species, four of them restricted to the southeastern corner near Costa Rica, is moderately rich in species. All except *D. standleyi* and *D. wendlandii* appear to range into the country from Costa Rica. The low species diversity and very low aroid endemism in *Dieffen-*

bachia in Middle America is perhaps explained by its historic remoteness from existing large land masses to the north and to the south. The distribution of modern aroid species suggests that the northwestern part of Middle America may have been isolated from Costa Rica in the area of the San Juan Depression (Nicaragua). Many of the species that occur in Costa Rica or Panama enter into Nicaragua in only a small area in the southeastern part of the country. Though the existing flora of Guatemala does not reflect isolation from Mexico to the same degree, it is possible that the more elevated portions of Guatemala, Nicaragua, and Honduras were isolated from major portions of Mexico by the Isthmus of Tehuantepec. With no endemic Mexican species, the *Dieffenbachia* flora reveals less endemism than does *Anthurium* (Croat, 1983a) or *Philodendron* (Croat, 1997). Both Mexican *Dieffenbachia* are relatively widespread, with *D. oerstedii* ranging to Panama (Fig. 29) and *D. wendlandii* ranging to Panama (Fig. 28).

The remaining Costa Rican and Panamanian species not already discussed above appear not to have strong affinities with South American species and clearly do not have affinities with other Central American species. On the other hand, there are some, relatively few, Central American species, among them *D. killipii*, *D. nitidipetiolata*, and *D. tonduzii*, that are likely to be of South American origin since they are wide-ranging species in South America.

Horticultural Significance

Dieffenbachia, like many other members of the Araceae, is one of the world's most important ornamental plants. Owing to the attractive leaves and hardiness under the difficult conditions found indoors, *Dieffenbachia* remains one of the most important ornamental plants in homes, offices, and professional displays. Ornamental aroids play a major role in the foliage-plant industry in the United States, making up about one-third of total foliage plant sales (Henny, 1988). *Dieffenbachia* is one of 5 aroid genera routinely among the top 10 foliage plants in annual sales volume (Henny, 1988).

The Araceae hold 7 of the top 13 positions in terms of overall sales in North America, including the first two (R. Henney, pers. comm.). An ornamental cultivar of *Dieffenbachia* is the second most important in sales, and the genus consistently has one or more taxa on the list of most popular ornamental plants in North America. *Dieffenbachia* breeding and culture plays a major economic role in the United States in Florida, California, and Hawaii.

Taxonomic Treatment

Dieffenbachia Schott, Wiener Z. Kunst 3: 820. 1829. TYPE: *Dieffenbachia seguine* (Jacq.) Schott.

Seguinum Raf., Fl. Tellur. 3: 66. 1836 [1837]. TYPE: *Seguinum maculatum* Raf. [= *Dieffenbachia seguine* (Jacq.) Schott].

Maguirea A. D. Hawkes, Bull. Torrey Bot. Club 75: 635. 1948. TYPE: *Maguirea spathicarpoides* A. D. Hawkes = [*Dieffenbachia paludicola* N. E. Br.].

Terrestrial; caudices thick, often elongate and prostrate, rooting at the lower nodes, the older portions of the stem trailing across the surface of the ground, often for considerable distances; sap often milky and frequently with varying concentrations of oxalic acid, with conspicuous annular leaf scars. *Petioles* elongate, amplexicaul, sheathed to the middle or sometimes to the apex; sheath unequal and often free-ending at apex; leaves clustered in a tight whorl at the stem apex; *blades* ovate to oblong-ovate, elliptic, oblanceolate, or obovate, acuminate at apex, acute to obtuse to rounded at base, typically subcoriaceous, sometimes variegated throughout or in areas along the midrib with paler colors; midrib raised on both surfaces; primary lateral veins pinnate, usually sunken above, raised below, much more prominent than the minor veins, all lateral veins extending to the margins without forming a single collective vein but with several primary lateral veins often forming a series of short, discontinuous collective veins; interprimary lateral veins sometimes present; minor veins distinct to obscure, usually not markedly raised, sometimes connected by transverse tertiary veins. INFLORESCENCES shorter than the leaves, 1 to several per axil; bracts short and usually inconspicuous; peduncle usually somewhat flattened and angular with one edge narrowed; *spathe* oblong, persistent, convolute at base, often somewhat constricted about midway, opening usually only above the middle, usually green on outside, somewhat paler within; *spadix* slightly shorter than the spathe, divided into pistillate and staminate portions, each with naked unisexual flowers; the pistillate portion basal, about as long as the staminate portion, fused to the spathe, remotely many-flowered (typically 20 to 80 rarely to 160); staminate portion clavate, white, free from the spathe, densely many-flowered, often separated from the pistillate portion by a naked interval. Staminate flowers consisting of 4 stamens united into a 4- to 5-sulcate, truncate synandrium; anthers lat-

eral, contiguous, the common connective thick, fleshy; the thecae obovoid to oblong-elliptic, dehiscing by short, apical, pore-like slits; pollen extruded in strands, inaperturate, ellipsoid or oblong or nearly spherical, large, averaging more than 75 µm, exine psilate to obscurely verruculate and/or sparingly punctate-foveolate to densely foveolate; pistillate flowers moderately dispersed but often in weak rows with 1 to 5(6) pistils per spiral, and surrounded by 4 or 5 claviform white staminodia, these longer than the ovary usually 2–5 mm, usually spreading, sometimes fused briefly at the base; ovaries 2- or 3-carpellate, sometimes 1-carpellate, sessile, depressed globose to depressed ovoid, 2- or 3-lobate; ovules 1 per locule, pale green, semiglossy, erect, anatropous; placenta axile to basal; stylar region inconspicuous; stigma large, hemispheric or 2- or 3-lobate, about as broad as the ovary, yellow to orange in color. INFRUCTESCENCE with fruiting spathe often turning yellow, orange, or red, breaking up longitudinally in fruit to expose the colorful berries; fruits baccate, globose or 2- or 3-lobed, 1- or 2(3)-seeded; seeds globose or ovoid, the testa thick, smooth, green to blackish green; embryo large; endosperm lacking.

Chromosomes $2n = 34, 68$.

Key to *Dieffenbachia* of Mexico, Central America, and the West Indies

1a. Petiole involute, extending to base of blade and frequently prolonged beyond the base of the blade.
  2a. Larger leaves regularly to more than 45 cm long and 23 cm wide, cuneate at base, coriaceous, usually glossy above, not variegated, uniformly green.
    3a. Petiole sheath markedly undulate, at least near the base; Atlantic slope.
      4a. Leaf blades matte and somewhat velvety to glisteningly velvety above, minutely wrinkled on upper surface; drying dark blackish brown to dark yellowish brown above; Atlantic slope of Panama ..... 21. *D. panamensis* Croat
      4b. Leaf blades semiglossy to glossy above and smooth on upper surface; drying medium gray to dark brownish gray above, paler and yellowish gray to pale yellow-brown below ..... 24. *D. standleyi* Croat
    3b. Petiole sheath not markedly undulate; Pacific slope ..... 13. *D. horichii* Croat & Grayum
  2b. Leaves rarely more than 45 cm long or 23 cm wide.
    5a. Primary lateral veins 6 to 7 per side; known only from the type locality in the Panama Canal area ..... 22. *D. pittieri* Engl.
    5b. Primary lateral veins usually 15 or more.
      6a. Leaf blades with primary lateral veins (10)15 to 17 per side; blade base obtuse to rounded; blade surface glossy to moderately glossy, not at all bullate, rarely variegated; petiole usually with a whitish band on the abaxial surface; Panama ..... 6. *D. crebripistillata* Croat
      6b. Leaf blades with primary lateral veins usually more than 18 per side; usually cordulate at base, usually matte and subvelvety above, usually bullate, often variegated; petiole lacking a whitish band on the abaxial surface; Nicaragua to Colombia ..... 25. *D. tonduzii* Croat & Grayum
1b. Petiole sheath erect to involute, ending short of blade base (except rarely on upper leaves).
  7a. Unsheathed portion of petiole usually triangular in cross section, sharply keeled to ridged abaxially, the margins thickly winged ..... 1. *D. aurantiaca* Engl.
  7b. Petiole beyond sheath subterete, rounded abaxially, with margins rounded to acute (not winged).
    8a. Plants with petioles or major veins of lower blade surface minutely granular-puberulent to puberulent.
      9a. Primary lateral veins 23 to 36 per side, departing midrib usually at about a 90° angle; midrib and primary lateral veins conspicuously puberulent with whitish trichomes ..... 2. *D. beachiana* Croat & Grayum
      9b. Primary lateral veins usually less than 18 pairs (rarely to 22 in *D. grayumiana*) usually departing midrib 40°–60° at blade midpoint; midrib and primary lateral veins inconspicuously granular-puberulent.
        10a. Blades narrowly oblanceolate, 6.4 times longer than wide, less than 6 cm wide ..... 5. *D. copensis* Croat
        10b. Blades elliptic to obovate-elliptic, oblong-elliptic, to narrowly oblong-lanceolate (rarely narrowly oblanceolate in *D. fortunensis*), 1.7–5.2 times longer than wide, 6.7–39 cm wide.
          11a. Petioles with sheaths ending no more than 5 cm from base of blade ..... 24. *D. standlevi* Croat
          11b. Petioles with sheaths ending more than 13 cm from base of blade.
            12a. Primary lateral veins arising at 30°–40° angle; central Panama ..... 10. *D. galdamesiae* Croat
            12b. Primary lateral veins arising at mostly 55°–70° (to 80° in *D. grayumiana*); Costa Rica and western Panama.
              13a. Plants usually stout, 1.5 m tall; blades narrowly ovate, (22) 30–54 cm long, 10–32 cm wide (averaging 36 × 18 cm), 1.5–2.6 times

longer than wide; Costa Rica to western Panama, 0–1300 m but mostly near sea level ..... 11. *D. grayumiana* Croat

13b. Plants medium-sized, rarely more than 1 m tall, usually less; blades mostly narrowly oblong-lanceolate, 15–33 cm long, 4.2–13 cm wide (averaging 21 × 6.8 cm), 2–6.3 times longer than wide; Panama (Chiriquí), 900–1600 m ..... 8. *D. fortunensis* Croat

8b. Plants with petioles or major veins of the lower blade surface glabrous.

14a. Petiole sheaths decurrent apically (lacking prominent protruding extensions); Atlantic lowlands.

15a. Blades drying blackened; Panama (Bocas del Toro), near sea level ..... 9. *D. fosteri* Croat

15b. Blades drying yellowish brown, greenish to yellowish brown.

16a. Petioles very glossy, drying as if covered with shellac; Nicaragua to Ecuador ..... 18. *D. nitidipetiolata* Croat

16b. Petioles not glossy, not drying as if covered with shellac.

17a. Plants less than 1 m tall; blades usually less than 10 cm wide ..... 12. *D. hammelii* Croat & Grayum

17b. Stems usually more than 1 m tall; blades more than 10 cm wide.

18a. Petioles matte; leaf blades usually subcordate at base, usually flecked with creamy yellow ..... 11. *D. grayumiana* Croat

18b. Petioles semiglossy; leaf blades cuneate to rounded or truncate at base, usually plain green (rarely mottled with pale green).

19a. Petioles terete; sheaths decurrent at apex, tightly inrolled with one side completely hidden by the other; Mexico to Panama but but primarily on Pacific slope (except in Oaxaca and Veracruz on Atlantic slope) ..... 26. *D. wendlandii* Schott

19b. Petioles usually obtusely sulcate, sometimes terete with an obtuse medial rib; sheaths open, the margins erect; Nicaragua to Colombia ..... 16. *D. longispatha* Engl. & K. Krause

14b. Petiole sheaths (at least on one side) rounded to auriculate at apex.

20a. Blades with more than 18 primary lateral veins or with primary lateral veins obscure, barely more conspicuous than interprimary veins.

21a. West Indian and South American species; plants with both sharply sulcate petioles and a thickened, protruding spadix; fruits 2- to 3-lobed ..... 23. *D. seguine* (Jacq.) Schott

21b. Mainly Central American species (*D. killipii*, *D. isthmia*, and *D. obscurinervia* also in South America).

22a. Blades with 10 to 13 pairs of primary lateral veins, these moderately inconspicuous, barely more obvious than interprimary veins; petioles and lower midribs with pale spots; Central Panama to Colombia ..... 19. *D. obscurinervia* Croat

22b. Blades with 18 to 28 pairs of primary lateral veins, decidedly more conspicuous than the interprimary veins; petioles and lower midrib lacking spots; Costa Rica, Golfo Dulce region ..... 3. *D. burgeri* Croat & Grayum

20b. Blades variously shaped, matte to glossy above, with 8 to 18 primary lateral veins per side.

23a. Spadix lacking medial sterile region, the male and female regions contiguous or nearly so.

24a. Petioles usually solid green, not densely and conspicuously pale-maculate.

25a. Blades with major veins on the lower surface granular-puberulent ..... 17. *D. lutheri* Croat

25b. Blades with major veins on the lower surface glabrous ..... 15. *D. killipii* Croat

24b. Petioles densely and conspicuously pale-maculate.

26a. Stems more than 1 cm thick; petioles never pale-maculate; primary lateral veins usually departing midrib at less than 90°; Costa Rica (Osa Peninsula), Panama, and Colombia ..... 15. *D. killipii* Croat

26b. Stems usually less than 1 cm thick; petioles distinctly pale-maculate; primary lateral veins usually departing midrib at 90° or more; Costa Rica, Sixaola region, Panama, and Colombia ..... 7. *D. davidsei* Croat & Grayum

23b. Spadix with an evident medial sterile region, pistillate and staminate portions separated by a distinct naked spadix axis.

27a. Plants usually less than 0.5 m tall ..... 20. *D. oerstedii* Schott

27b. Plants to more than 0.5 m tall.

28a. Blades drying dark brown to blackened on upper surface.

29a. Blades usually with posterior lobes; lower blade surface drying

yellowish brown to yellowish gray-brown to dark yellow-brown or yellowish green; stems solid dark green, drying glossy and minutely wrinkled (the areoles interspersed with raphide cells); Panama, Veraguas Province and the Azuero Peninsula in the west (at 700–900 m in Herrera and Los Santos Provinces) to Darién Province in the east, and to Colombia 50–800(1000) m ..... 14. *D. isthmia* Croat

29b. Blades lacking posterior lobes; lower blade surface drying grayish black; stems mottled dark green, drying smooth with a dense layer of raphide cells (but not minutely wrinkled); Panama, Bocas del Toro, sea level ..... 9. *D. fosteri* Croat

28b. Blades drying yellowish green to dark gray-green, rarely brownish on upper surface.

30a. Petioles usually white at base; blades usually less than 20 cm long ..... 20. *D. oerstedii* Schott

30b. Petioles not whitish at base, frequently paler than stem but not markedly paler than the remainder of the petiole; blades usually more than 20 cm long.

31a. Petioles usually sharply C-shaped, discolored and whitish at the base; blades matte ..... 20. *D. oerstedii* Schott

31b. Petioles terete to obtusely C-shaped or obtusely D-shaped, not sharply sulcate, not discolored and whitish at base; blades glossy to semiglossy.

32a. Species of mostly dry habitats in western Central America (Mexico to Panama); blades subcoriaceous, semiglossy on upper surface, (15)20–55(65) cm long (averaging 35 × 17 cm); 75 to 900 m in elevation ..... 26. *D. wendlandii* Schott

32b. Species of wet habitats, southeastern Nicaragua and along the entire Atlantic slope and the Osa Peninsula of Costa Rica; blades moderately coriaceous, glossy on the upper surface, 16–36 cm long, (averaging 23 × 12 cm); sea level to 200 m, mostly at less than 100 m in elevation ..... 4. *D. concinna* Croat & Grayum

1. Dieffenbachia aurantiaca Engl., Anales Inst. Fis.-Geogr. Nac. Costa Rica 9: 209. 1898. TYPE: Costa Rica. Puntarenas: "in silvis prope Santo Domingo ad sinum dulcem [Santo Domingo de Golfo Dulce], fructif. Mart. 1896," *A. Tonduz 9961* (holotype, B!; isotypes, CR!, US!). Figures 2, 27A.

Stout herb, 0.7–2.3 m tall; sap fetid and caustic; stems erect at apical part, to 2 m long, the older portion reclining and up to 2 m long; internodes 2.0–4(6) cm long, 5–7(10) cm diam., dark green to pale green, semiglossy to glossy, streaked with paler green; *petioles* 13–33(48) cm long (averaging 24 cm long), C-shaped at base in cross section, moderately spongy, medium green, semiglossy adaxially, matte and acutely 1-ribbed abaxially, the surface finely dark striate, sometimes variegated with paler green markings, sheathing ⅓ to nearly throughout (35%–97% their length and averaging 77%); sheath 6.5–25.5(38) cm long (averaging 17.7 cm), medium green, finely dark green striate, sometimes variegated with paler green markings, adaxially acute margins sometimes much paler, with margins incurled but usually not overlapping, the apex free-ending and obliquely rounded to rounded-auriculate distally; unsheathed portion 0.5–2 cm long, angular to ± triangular in cross section, flat to broadly sulcate adaxially (sometimes with a medial keel), adaxial margins thin and revolute, acutely keeled abaxially, abaxial margins thickly winged, sometimes with a medial keel, thin, revolute, sometimes medially keeled at margins; *blades* oblong-elliptic to ovate-elliptic, slightly inequilateral, one side 1–1.5 cm wider than the other side, usually subcoriaceous, acuminate to abruptly acuminate at apex, slightly inequilateral and obtuse to rounded or subcordate (rarely attenuate on one side) at base, (26)31–57 × 11–27 cm (averaging 39 × 19 cm), 1.7–2.6 times longer than wide (averaging 2 times), ranging from about as long as petioles to 2.8 times longer than petioles (averaging 1.7 times longer); margins weakly undulate; upper surface dark green, concolorous or sometimes variegated, drying dark olive-green to medium gray-green, weakly glossy to semiglossy; lower surface moderately paler, matte to weakly glossy, drying pale yellowish green; midrib flat to broadly concave above (broadly sulcate near base), 5–20 mm diam., sometimes

Figure 1. —A. *Dieffenbachia longispatha*, spathe blade showing open position at anthesis with thrips present on inner surface of spathe (*Croat & Zhu 77042*). —B. *Dieffenbachia tonduzii*, inflorescence at anthesis showing fully opened spathe with beetles in base of spathe tube and partially eaten sterile staminate flowers (*Croat & Zhu 76653*). —C. *Dieffenbachia wendlandii*, close-up of inflorescence showing intact unilocular pistils with mostly eaten staminodia (edge of spathe tube partially removed) (*Croat 39749*). —D. *Dieffenbachia wendlandii*, mature infructescence showing exfoliated spathe and berries splayed out for display (*Croat & D. Hannon 65536*).

whitish, faintly striate above, bluntly acute to V-shaped (a continuation of the triangular petiole) below, drying brown below, faintly striate; primary lateral veins (8)12 to 14 per side, departing midrib at a steep angle, spreading at a 50°–70° angle, gradually spreading in a broad curve, slightly to moderately paler than surface in the proximal one-half, weakly raised to convex in valleys, flat and darker than surface toward margins, drying mostly paler, sometimes darker than surface above, weakly convex and slightly paler than surface below, drying yellowish and paler than surface or brownish and darker than surface below; interprimary veins present or absent, usually with 1 between each pair of primary lateral veins in the lower ⅓ of the blade; minor veins darker than surface, visible but moderately obscure below. INFLORESCENCES to 3 per axil; peduncle (7)10–18 cm long, acutely angular on one side, drying striate, 3–6 mm diam.; *spathe* 17–25(38) cm long, 2–3.5 cm wide, flattening to 5.7–8 cm wide on tube, 2.5–6.5 cm wide at constriction, 3–4.3 cm longer than the spadix, gradually long-tapered toward apex from the middle, uniformly light green to medium green throughout; weakly glossy outside, glossy inside; spathe blade 2.5–7 cm wide when flattened; *spadix* 16–20(33) cm long; free portion to 15.5 cm long; pistillate portion 6.5–8.5(15.5) cm long, 1.5–2 cm diam. throughout (mostly drying 6–9 mm diam.); fertile staminate portion 7–12.5 cm long, white, tapered toward apex and weakly tapered slightly toward base; intermediate sterile segment 1.5–4 cm long, with a few scattered pistils in lower half and a few scattered staminodia in upper half; pistils 51 to 72, irregularly scattered, with 3 to 4(6 to 7) across the width of the spadix, separated from one another by ½ to 4.0 times their width, depressed-globose, to 2 mm long, 1.2–1.6(2.8) mm diam., pale green; stigmas cushion-shaped, to 2 mm high, 2.5–3 mm wide, white; staminodia 3 to 5 per pistil, 1.5–2(3.8) mm long, free or briefly united at base, held well above the stigmas sometimes united for much of their length; synandria 1–2(3.4) mm diam., margins irregularly angled with rounded, linear to 3-sided slit medially at apex. INFRUCTESCENCE 19–24 cm long; spathe orange outside; spadix 8–15 cm long; berries red-orange, B & K yellow-red 6/2.5 to B & K yellow-red 7/5 to red B & K red 6/10 (Berlin & Kay, 1969), subglobose, ovoid to ellipsoid, 7–10 mm long.

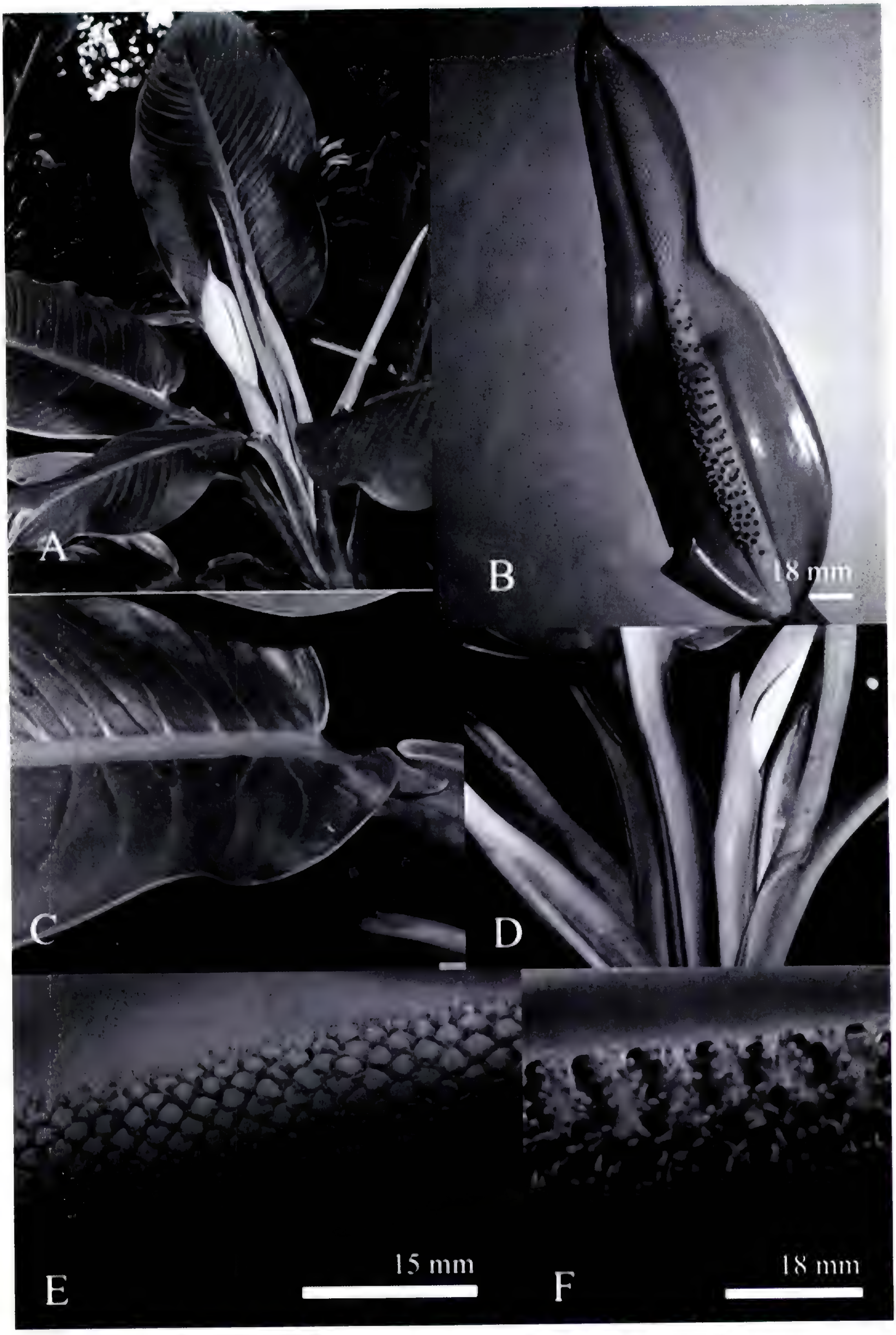
Distribution and habitat. *Dieffenbachia aurantiaca* is known only from southwestern Costa Rica and adjacent Panama, in the region of the Osa Peninsula in Costa Rica and the Burica Peninsula in Panama. It occurs in wet forests and swampy sites from near sea level to 780 m in *Tropical wet forest* (T-wf) and *Premontane wet forest* (P-wf) life zones (Holdridge, 1967).

Phenology. *Dieffenbachia aurantiaca* begins to flower in the early rainy season with flower buds having been seen as early as May and as late as August, and mature open inflorescences seen between May and December. Fruiting occurs between September and March.

Discussion. The species is characterized by its more or less elliptic, usually unvariegated, green-drying blades, obtuse to subcordate at base, but especially by the triangular and weakly sheathed petioles, decurrent at apex. It is probably most closely related to *D. horichii*, but differs from that species in having a longer free portion of the petiole, which is more or less triangular. Also vegetatively similar are *D. longispatha* and *D. nitidipetiolata*, but both differ primarily for the same reasons, i.e., that the free portion of the petiole is not triangular.

An unusual collection, *Croat 67700*, from a relatively dry area on the Pacific slope of Costa Rica (drier than the typical sites for this species), has a petiole that is described as terete though the collection otherwise matches *D. aurantiaca*. The collection looks vaguely like *D. nitidipetiolata*, which is otherwise found only on the Atlantic slope. A Tonduz collection at US originally labeled *Tonduz 9961*, was relabeled *7177* despite the fact that it was also collected in March 1896. It appears to be identical to two other specimens labeled *Tonduz 9961*, the type collection number.

Additional specimens examined. COSTA RICA. 18XX. *Pittier & Durand s.n.* (BR). **Puntarenas:** near Palmar Norte, *Allen 5972* (UC); Playa Blanca, Golfo Dulce, *Valerio 462* (CR, F); Golfo Dulce-Río Terraba, *Skutch 5328* (US); Cantón de Osa, Buenos Aires, Fila Retinto, from Palmar Norte to Jalisco, *Grayum & G. Herrera 9139* (CR, MO); Pan-Am Hwy. 287 (ca. 3 km NW of Chacarita & 30 km S of Palmar Sur), *Grayum et al. 7549* (MO); near Pan-Am Hwy. vic. Piedras Blancas, *Croat 32955* (HUA, INB, MO); W side of Fila Gamba, ca. 6 km from Golfito airport, *Croat & Grayum 59906* (CR, MO); Cantón de Golfito, Par. Corcovado, vic. Estación Sirena, 14 Apr. 1995, *Picado & Gamboa 138* (INB, MO); Piedras Blancas-Rincón (on Osa Peninsula), 3.7 mi. W of Pan-Am Hwy., *Croat 67700* (MO); San Vito de Coto Brus to Ciudad Neily, NE slopes of Fila de Cal, *Hammel & Grayum 14169* (MO); Palmar Norte-Panama border, 3 km N of turn-off to Rincón, *Croat & Hannon 79193* (COL, INB, MEXU, MO, UB, WU); Osa: 2 km N of Chacarita, S of Palmar Norte, *Maas et al. 7834* (INB, MO, U). **San José:** N of Palmar Norte, trail to Jalisco, *Croat 35210* (F, MO); 5 km W of Palmar Norte on rd. to Puerto Cortes, *Lent 161* (F, NY, US); San Isidro del General-Dominica, ca. 1 mi. beyond divide, *Croat 35292* (INB, MO). PANAMA. **Chiriquí:** Puerto Armuelles, *Woodson Jr. & Schery 861* (F, MO); Puerto Armuelles-San


A
B
18 mm
C
D
E
15 mm
F
18 mm

Bartolo Limite, 7 mi. W of Puerto Armuelles, *Croat 35079* (MO); Burica Peninsula, 8 km W of Puerto Armuelles, *Croat 21961* (F, MO); Quebrada Manzanillo, 9 km S-SW of Puerto Armuelles, *Busey 743* (MO); Quebrada Quanabanito beyond La Represa, 2 mi. SW of Puerto Armuelles, *Liesner 114* (MO, US).

2. Dieffenbachia beachiana Croat & Grayum, Novon 9: 492. 1999. TYPE: Panama. Bocas del Toro: Chiriquí Grande-Fortuna, 13.2 mi. W of Chiriquí Grande, 8°45′N, 82°10′W, 310 m, *T. B. Croat & M. H. Grayum 60130* (holotype, MO-323065!; isotypes B!, K!, PMA!, US!). Figures 3, 28B.

Slender herb, 40–100 cm tall; stems briefly creeping at base; *internodes* 2–6 cm long, 1.5–3.5 cm diam., medium green to olive-green, sometimes streaked with cream, semiglossy and obscurely roughened. LEAVES clustered near stem apex, erect-arching; *petioles* 17–46 cm long (averaging 26.5 cm long), sheathed 25%–83% of petiole (averaging 54%); sheath 10–22 cm long (averaging 14.2 cm), decurrent at apex; unsheathed portion (2.5)10–30 cm long, broadly C-shaped in cross section, dark green to brownish, flattened with acute, erect margins or sharply to bluntly sulcate adaxially, surface pale green-mottled, matte, usually minutely roughened and with scattered scales, whitish raphide cells visible, drying with scattered clusters of pustular raised areas with granular-puberulent protrusions; *blades* narrowly elliptic to lanceolate, rarely narrowly ovate, inequilateral, one side 1–2 cm wider than the other side, thinly coriaceous to subcoriaceous, drying papyraceous, weakly bicolorous, ± equilaterally acuminate at apex (the acumen to 5 mm long), slightly inequilateral and acute, rounded or truncate (rarely subcordate in Panama) at base, 16–41 cm long, 6.5–15 cm wide (averaging 28 × 10.7 cm), 1.8–5.3 times longer than wide (averaging 2.6), 0.7–1.9 times longer than petioles (averaging 1.12 times longer than petioles); margins crisped-undulate; upper surface dark green (in Panama sometimes mottled with white or cream), semiglossy (rarely matte), lower surface semiglossy to weakly glossy or matte, slightly paler; midrib flat-raised above, often striate, usually concolorous above, convex to thicker than broad below, puberulent with thick, whitish trichomes below; *primary lateral veins* 23 to 30(36) per side, departing midrib at a 70°–110° (to 45° toward apex and sometimes at base) angle, arising acutely then straight to weakly curved to the margins (then sweeping prominently toward apex), usually quilted-sunken above, convex, puberulent with thick, whitish trichomes, sometimes with adjacent veins alternating ascending and descending below; interprimary veins usually present, scarcely less visible than primary lateral veins; minor veins moderately distinct and weakly raised below. INFLORESCENCES 1 to 3 per axil; *peduncle* 9–13 cm × 5–7 mm, drying 3–4 mm diam.; *spathe* 10–19 cm long, gradually constricted at middle, green throughout, gradually long-tapered to apex; spathe blade to 3 cm diam. when flattened; spathe tube 1–2 cm diam.; *spadix* 13–15 cm long; pistillate portion 4.5–6 cm long, drying 7 mm diam. throughout; fertile staminate portion 5–6.5 cm long, drying 4 mm diam. throughout; intermediate mostly sterile portion usually 2–3.5 cm long, 2 mm diam., sometimes with pistillate and staminate portions almost contiguous; pistils 46 to 66(100), 2 to 4 situated across the width of the spadix, ovary oblong-ellipsoid, 1.5–2 × 1–1.6 mm; stigmas subglobular, about as broad as the ovary; staminodia narrowly clavate, usually not at all fused at base, ca. twice as long as pistil; synandria 1.8–2.6 mm diam., margins irregularly subrounded, drying smooth and light brown at apex. INFRUCTESCENCE with spathe (10)14–16 cm long, somewhat flattened, yellow-green mottled green and white with darker flecking, maturing to orange; spadix 6–10 cm long; *berries* orange, subglobose, 6–8 mm diam.

Distribution and habitat. *Dieffenbachia beachiana* ranges from northeastern Costa Rica to western Panama (Bocas del Toro, Chiriquí, and Veraguas) at elevations of 40 to 800 m. In Costa Rica it occurs on the Atlantic slope of the Central Cordillera and the Cordillera Talamanca, ranging from the Sarapiquí region to Tortuguero and Siquirres.

Phenology. *Dieffenbachia beachiana* initiates inflorescences in the late rainy season with plants reaching anthesis in the dry season (January through April). Immature fruits have been seen from April to September and mature fruits have been seen from April to December.

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Figure 2. *Dieffenbachia aurantiaca* (*Croat 35292*). —A. Habit, showing open inflorescence. —B. Close-up of spathe and spadix (spathe held in a fully splayed position). —C. Close-up of leaf showing fully sheathed petiole. —D. Leaf cluster with open spathe, showing side view. —E. Close-up of portion of spadix with pistils showing stigmas and the overtopping club-shaped staminodia. —F. Close-up of staminate portion of spadix showing strands of pollen emerging from between androecia.

Figure 3. *Dieffenbachia beachiana.* —A. A series of leaves showing adaxial surface (*Croat 44283*). —B. Close-up of leaf cluster showing variegated leaves and a cluster of inflorescences (*Sims 8*). —C. Adaxial surfaces of leaves and open inflorescences. —D. Close-up of inflorescence showing emergent portion of the spadix and adaxial surface of petiole. C, D. (*Croat 68444*).

Discussion. The species is characterized by its moderately thin, quilted blades with many broadly spreading primary lateral veins and crisped-undulate margins with the lower midrib and primary lateral veins puberulent. *Dieffenbachia beachiana* is similar to *D. galdamesiae*, a species from central Panama that also has somewhat puberulent midribs on the lower blade surfaces. That species differs in having the pubescence much shorter, merely granular-puberulent, and has fewer than 22 veins per side (vs. 23 to 36 for *D. beachiana*) that arise from the midrib at a 30°–40° angle (vs. 70°–110°). In addition, Panamanian populations of *D. beachiana* differ in having their blades usually white- to cream-mottled, whereas those of *D. galdamesiae* are always solid green in color. *Dieffenbachia beachiana* is also somewhat similar to *D. grayumiana*, but that species differs in having the veins merely minutely granular in slender rows on drying, and in having somewhat more ovate and wider blades.

A single collection (*Croat 66953*) from Veraguas Province in Panama differs in having the primary lateral veins curving more prominently toward the apex than material from elsewhere in western Panama and Costa Rica. In addition, the pubescence is merely granular-puberulent rather than puberulent. *Hammel 9660*, collected at La Selva in Heredia Province in Costa Rica, probably represents a hybrid between *D. beachiana* and *D. concinna*. The specimen has the slightly scabrous petioles and the impressed major veins of *D. beachiana*, but the blades are more or less elliptic and dry the color of *D. concinna*.

Additional specimens seen. COSTA RICA. **Heredia:** Río Peje-Río Sardinalito, Atl. slope of Volcán Barva, *Grayum 6899* (MO); San José-Pto. Viejo, vic. of Chilamante, 11.6 mi. N of Cariblanco, *Croat 68358* (B, CR, MO); Finca La Selva, near Río Puerto Viejo, *Burger & Stolze 5754* (CR, F); Zona Protectora, N slopes of Volcán Barba, Río Peje-Río Guacimo, *Grayum & Schatz 3220* (DUKE). **Limón:** Río Pacuare-Quebrada Diablo, ca. 2.5 km E of Siquirres, *Grayum 7698* (MO); Par. Tortuguero, Est. Agua Fría, *R. Robles 1234* (CR, MO); La Colombiana Farm, United Fruit Co., *Standley 36840* (US). **Puntarenas:** Golfito, Par. Nac. Esquinas, Quebrada Gamba, *Sanchez 539* (MO). **San José:** Vazquez de Coronado, Braulio Carrillo NP, along hwy. San José to Siquirres, trail to Río Sucio, *Croat 78771* (INB, MO, WU). PANAMA. **Bocas del Toro:** Chiriquí Lagoon, Water Valley, *von Wedel 1438* (MO); 10 km SW of Chiriquí Grande, *Thompson 4937* (CM); Fortuna Dam-Chiriquí Grande, 7.3 mi. N of bridge over Fortuna Dam, 3.2 mi. N of Continental Divide, *Croat & Grayum 60255* (MO); Chiriquí Grande-Fortuna, 7.7 mi. W of Chiriquí Grande, 1.5 mi. W of Punta Peña, *Croat & Grayum 60094* (K, MO, SCZ); near hwy. to Chiriquí Grande, *McPherson 11816* (MO). **Veraguas:** vic. of Santa Fe, 8 mi. N of Escuela Circlo Alto de Piedra, *Croat 66953* (MO, PMA, SCZ, US).

Cultivated specimens. Costa Rica. *Henny 5* (MO). Heredia: Finca La Selva, O.T.S. Field Station, originally collected by Jim Beach, cultivated at Missouri Botanical Garden (MBG), vouchered as *Croat 59152* (MO).

3. Dieffenbachia burgeri Croat & Grayum, sp. nov. TYPE: Costa Rica. Puntarenas: Palmar Norte-Panamanian border, 3 km N of turn-off to Rincón, 8°48′39″N, 83°16′18″W, 110 m, 10 Sep. 1996, *T. B. Croat & D. Hannon 79211* (holotype, MO-5170493!; isotypes, AAU!, B!, CAS!, CR!, COL!, DUKE!, EAP!, F!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, PMA!, RSA!, US!, VEN!, UB!, WU!). Figures 4, 27B.

Planta terrestris, 0.5–1 m; internodia 0.5–2.0 cm longa, 1.2–2.5(3.5) cm diam.; petiolus 13–48 cm longus, vaginatus ⅓–⅔ longitudinis; vagina 8.5–20 cm longa, inequilateralis acute ad apicem apex; pars libera 5.3–29.5 cm longa; lamina oblongo-lanceolata vel anguste elliptica, 25–40 cm longa, 5–16 cm lata, nervis primariis lateralibus (13)18–28 utroque; inflorescentia 1–7 in quoque axilla; pedunculus 7.5–12 cm longus; spatha 11.5–15(21) cm longa; spadix 9–15.6 cm longus; pistilla 21–37.

Herb, 0.5–1 m tall, sap milky, sharply foetid; *internodes* glossy to semiglossy, drying frequently matte and minutely warty, 0.5–2 cm long, 1.2–2.5(3.5) cm diam., dark green to blackish green, drying dark brown to black or yellow-brown or yellow-green. LEAVES scattered along stem with areas exposed except near apex; *petioles* 13–48 cm long (averaging 26 cm long), dark green, surface somewhat mottled, weakly pale-streaked near base, glossy to semiglossy, sheathing ⅓ to ⅔ the length of the petiole (0.5 their average length); sheath 8.5–20 cm long (averaging 12.6 cm), sometimes solid creamy white, with margins often drying thin and light brown, the tip inequilaterally acute; unsheathed portion 5.3–29.5 cm long (averaging 12.9 cm), variable in cross section, from subterete to C-shaped or U-shaped, sharply sulcate to somewhat flattened near apex adaxially, the margins obtuse to acute; *blades* oblong-lanceolate to narrowly elliptic, 25–40 cm long, 5–16 cm wide (averaging 30.5 × 10.5 cm), 1.9–3.7 times longer than wide (averaging 2.8 times longer than wide), 0.83–1.6 times longer than petiole (averaging 1.21 times longer), slightly inequilateral, one side 0.4–1.4 cm wider than the other side, thinly coriaceous to subcoriaceous, slightly to moderately bicolorous, gradually long acuminate at apex, narrowly acute to rounded and equilateral or slightly inequilateral at base (one sometimes up to 6 mm higher on the midrib than the other); upper surface solid dark green, matte to weakly glossy (sometimes variegated with pale mottling), drying gray-green to dark olive-green; lower surface slightly paler, semiglossy to weakly glossy

Figure 4. *Dieffenbachia burgeri*. A, C, D. (*Croat & D. Hannon 79211*). —A. Side view of whole plant showing roots, stem, leaves, and inflorescences. —B. (*Croat & Grayum 59814*). Cultivated collection with open inflorescence. —C. Close-up of inflorescence with spathe cut open. —D. Mature infructescences, one open with berries exposed.

(sometimes matte or weakly glossy on both surfaces), drying medium yellow-green to yellow-brown; *midrib* above flat to sharply sulcate, sometimes flat-raised, 3–5 mm wide, semiglossy, concolorous, drying slightly darker than surface; convex to thicker than broad below, convex toward apex, slightly paler than surface, drying dark brown to yellow-brown, often acutely 1-ribbed; *primary lateral veins* (13)18 to 28 per side, departing midrib at an acute angle, then spreading at (40°)45°–70° angle, sweeping along margin, not forming collective veins, sunken to quilted above, convex beneath, drying darker or lighter than surface; the interprimary veins slightly less prominent than primary lateral veins; minor veins moderately close and darker than surface (drying weakly raised); surface minutely speckled on drying. INFLORESCENCES 1 to 7 per axil; *peduncle* 7.5–12 cm × 4 × 7 mm, medium green, moderately glossy (sap with a faint, unusual scent); *spathe* 11.5–15(21) cm long at anthesis, 1.1–1.9 cm longer than the spadix, glossy to semiglossy on both surfaces, flattening 2.7–3 cm diam. at constriction, dark green outside throughout, slightly paler inside; spathe blade < 2 cm diam. when furled; spathe tube to 10 cm long, 1.5–2.0 cm diam., flattening 3.7–7 cm wide; spathe blade 2.7–3.7 cm diam. at anthesis; *spadix* 9–15.6 cm long at anthesis; free portion 4–8.7 cm long; pistillate portion 5–6 cm long; the fertile staminate portion 4–6.5 cm long, 5–6 mm diam., directed slightly forward out of the spathe; sterile intermediate segment 1.5–3 cm long, 5 mm diam., with many staminodia near base and few just below fertile staminate portion; pistils 21 to 37, moderately closely spaced, almost contiguous, to 3 dispersed across spadix width, weakly constricted below middle, green to pale yellow; stigmas pale yellow, 1–1.5 mm on drying; staminodia about as long as or slightly longer than pistils, somewhat flattened and thickly swollen, subglobular and somewhat truncate at apex; synandria drying irregularly somewhat rounded, the margins usually irregularly turned upward, 1–1.4 mm diam. at apex, orange to yellow-orange, green, narrowly angled on one side. INFRUCTESCENCE with spathe usually orange; fruiting spadix 5–7 cm long, ca. 3 cm wide; *berries* orange-red to red-orange drying pale yellow-brown, ovoid, 7–8 mm long; seeds drying blackened, minutely warty.

Distribution and habitat. *Dieffenbachia burgeri* is endemic to southwestern Costa Rica on the Pacific slope from Dominical to the Osa Peninsula, sea level to 500 m, rarely 1000 m elevation, in *Tropical wet forest* (T-wf), *Premontane wet forest* (P-wf), and sometimes in *Premontane rain forest* (P-rf) life zones (Holdridge, 1967). It occurs in wet forests and swampy sites.

Phenology. Flowering in *D. burgeri* occurs in the late wet season to early dry season from November to March, and mature fruits have been seen from early April to early October.

Discussion. The species is characterized by the petiole sheathed ⅓–⅔ of its length, with the sheath acute at the apex; and the usually matte, greenish-drying leaf blades with numerous primary lateral veins. The blades are quite variable, ranging from narrowly oblong-elliptic to ovate-elliptic, oblong-lanceolate or narrowly elliptic. *Dieffenbachia burgeri* is most easily confused with *D. oerstedii* and differs from that species in having the petiole sheath acute at the apex, rather than free-ending and rounded to auriculate as in *D. oerstedii*. In addition, *D. burgeri* has more primary lateral veins, numbering (13)18 to 28 per side (vs. (4)6 to 9(11) per side in *D. oerstedii*).

Burger & Liesner 7254 describes the spathe at anthesis as having a strong unpleasant aroma.

Etymology. The species is named in honor of William Burger of the Field Museum of Natural History, long-time expert on Costa Rican plants, who made the first collection of the species as well as most of the earliest collections during his expeditions to Costa Rica.

Paratypes. COSTA RICA. **Puntarenas:** Palmar, Sur-Chacarita km 287, ca. 3 km NW of Chacarita, *Grayum et al. 7547* (INB, MO); Refugio Nac. Golfito, Fila Gamba, Río Cañaza drainage, *Grayum & G. Herrera 9236* (CR, MO); Fila Barriganes, ca. 1 km S, 3 km W of Cañasas, *Croat & Grayum 59814* (COL, CR, INB, MO, PMA, QCNE, SCZ, TEFH, US); Piedras Blancas Rincón 3.7 mi. W of Pan-Am Hwy., *Croat 67692* (MO); Chacarita-Rincón de Osa, ca. 6 km W Chacarita, *Croat & Grayum 59731* (CR, MO); Rincón de Osa, ridge betw. Quebrada Aparicio-Quebrada Aguabuena, *Grayum et al. 4014* (CR, MO); W of Rincón de Osa, *Croat & Grayum 59851* (MO); Par. Nac. Sector Esquinas, vic. of Fila Gamba hills behind Esquinas Rain Forest Lodge, along Quebrada Negra, at end of side rd. off of Villa Bricena to Golfito Rd., *Croat & D. Hannon 79286* (CM, INB, MO); San José, along rd. to San Isidro del General, *Burger et al. 10671* (F, MO); Golfito, Quebrada Negra, *Marten 848* (F); Osa, ca. 5 km W of Rincón de Osa, *Burger & Gentry Jr. 8898* (CR, F); near the airfield ca. 4 mi. W of Rincón de Osa, *Burger & Stolze 5489* (F); W of airstrip, *Utley & Utley 1100* (CR, F). **San José:** Pérez Zeledon Cantón, San Isidro General-Dominical, Fila Tinamastes, *Croat & D. Hannon 79112* (INB, MO, QCNE, USM); San Isidro del General-Dominical, above Alfombra, *Burger & Baker 10121* (F, MO).

4. **Dieffenbachia concinna** Croat & Grayum, Novon 9: 492. 1999. TYPE: Costa Rica. Puntarenas: Palmar Norte-Panamanian border, 3 km N of jct. to Rincón, 8°48′39″N, 83°16′18″W, 110 m, 10 Sep. 1996, *T. B. Croat & D. Hannon*

79191 (holotype, MO-5170498!; isotypes, AAU!, B!, CAS!, COL!, CR!, DUKE!, F!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, PMA!, US!). Figures 5, 28A.

Small, erect herb, 0.6–1.3 m tall, sap milky; internodes glossy, 1.5–4(7.5) cm long, 1–4 cm diam., medium green to dark green, obscurely marbled light to medium green. LEAVES erect-arching; *petioles* 7.5–25(35) cm long (averaging 17 cm long), terete and obtusely sulcate near apex or subterete to C-shaped or D-shaped in cross section, flat to shallowly sulcate adaxially (the margins obtuse to acute), rounded or sometimes acute abaxially, moderately erect, semiglossy or almost matte, dark green to olive-green, blotched striate or streaked white or silver-green, drying green to sometimes light yellow-brown, sheathing from lower ⅖ to nearly throughout (averaging 0.63 of length); sheath 6.7–13(20) cm long (averaging 9.5 cm), to 1.5 cm diam., margins erect to involute, the tip asymmetrically auriculate to rounded and free-ending, with one side obtuse to rounded, with the other side acute to obtuse; unsheathed portion 1–13 cm long, to 1.5 cm diam.; *blades* usually ± elliptic, ovate-elliptic, rarely ovate or broadly lanceolate, 16–36 cm long (averaging 23 cm long), (7.8)10–15.5(20.5) cm wide (averaging 12 cm wide), 1.5–2.9 times longer than wide, broadest usually at or near middle, 0.8–2.4 times longer than petiole, equilateral to slightly inequilateral, one side to 1 cm wider than the other side, equilaterally acuminate at apex, the acumen sometimes apiculate, broadly acute or usually rounded, slightly inequilateral at base, moderately coriaceous, weakly to moderately bicolorous; upper surface semiglossy to glossy, dark green or rarely white to cream or yellow-green splotched or flecked, drying dark olive-green, dark gray-green to yellowish brown; lower surface moderately paler, matte to weakly glossy, green, rarely dark gray-green, drying yellowish brown to green, rarely dark gray-green; *midrib* flat to broadly flat-convex and concolorous to paler than surface above (sometimes paler in distal ⅓ above), low-convex to convex or rounded-triangular, slightly paler than surface below, drying light brown to dark brown with medial portion usually drying darker; *primary lateral veins* 6 to 12(14) per side, spreading from midrib at a 45°–70° angle (sometimes arising at an acute angle), only rarely at different angles on opposite side of blade, weakly sunken above, convex to obscurely raised below; the interprimary veins sometimes visible, 1 between each pair of primary lateral veins; minor veins indistinct to visible and darker than surface below. INFLORESCENCES 2 to 8 per axil; *peduncle* (2.5)8–17.5 cm long (averaging 10.5 cm long), somewhat compressed dorsiventrally in cross section, 3–4 mm wide on drying; *spathe* 11–25.7 cm long, 1.5–2.0 cm wide when furled (as long as or up to 2 times longer than peduncle and averaging 1.6 times longer), constricted 4.5 cm above base, the constricted area 1.8–3 cm wide when flattened, medium to pale green outside, somewhat darker on tube except white on open face, uniformly paler within, drying dark brown to blackened throughout; spathe blade 3.3 cm wide when flattened; spathe tube 4.5–8.5 cm wide when flattened, paler inside; *spadix* protruding forward at anthesis, 12–14 cm long; free portion 6.5–9.5 cm long; pistillate portion tapered toward apex, 4.5–9 cm × 5–12 mm, stipe and axis pale green; fertile staminate portion white, tapered slightly toward both ends, 8–9 cm long, 7–10 mm diam. midway; sterile staminate portion 2.5–4 cm long; mostly sterile intermediate segment 5–7 mm diam., mostly bare but with a scattering of staminodia on both ends (especially at base); pistils 42 to 65, closely spaced; ovary globose, 1–2.5 mm diam., pale green; stigma pale yellow; staminodia 1–5 mm long, up to 3 times longer than pistil, somewhat flattened toward base and free at base, tapering and somewhat globular, 1–2 mm diam. at apex; synandria with flowers irregularly rounded, 0.8–1.4 mm diam. INFRUCTESCENCE with spathe yellow-orange to bright orange outside; spadix to 6–8 cm long; *berries* bright red to orange-red, oblong-ellipsoid, to 1 cm long, 8 mm diam.

Distribution and habitat. *Dieffenbachia concinna* ranges from southeastern Nicaragua along the entire Atlantic slope to the Osa Peninsula of Costa Rica, sea level to 200 m, mostly < 100 m, sometimes locally common in rocky sites along streams.

Phenology. Flowering in *D. concinna* occurs mostly during the middle of the rainy season, from July through November (rarely December), especially September and October. A cultivated collection at the Missouri Botanical Garden flowered repeatedly over a two-week period during late May and early June. Collections with immature fruits have been seen from December to March. Mature fruits occur primarily December through June, especially January to May but with one fruiting collection each seen in August and September.

Discussion. The species is recognized by the glossiness of all parts of the plant; its relatively small stature; moderately coriaceous, more or less elliptic, weakly inequilateral blades; and auriculate petiolar sheaths. It is most easily confused with *D. oerstedii*, but differs from that species in its larger

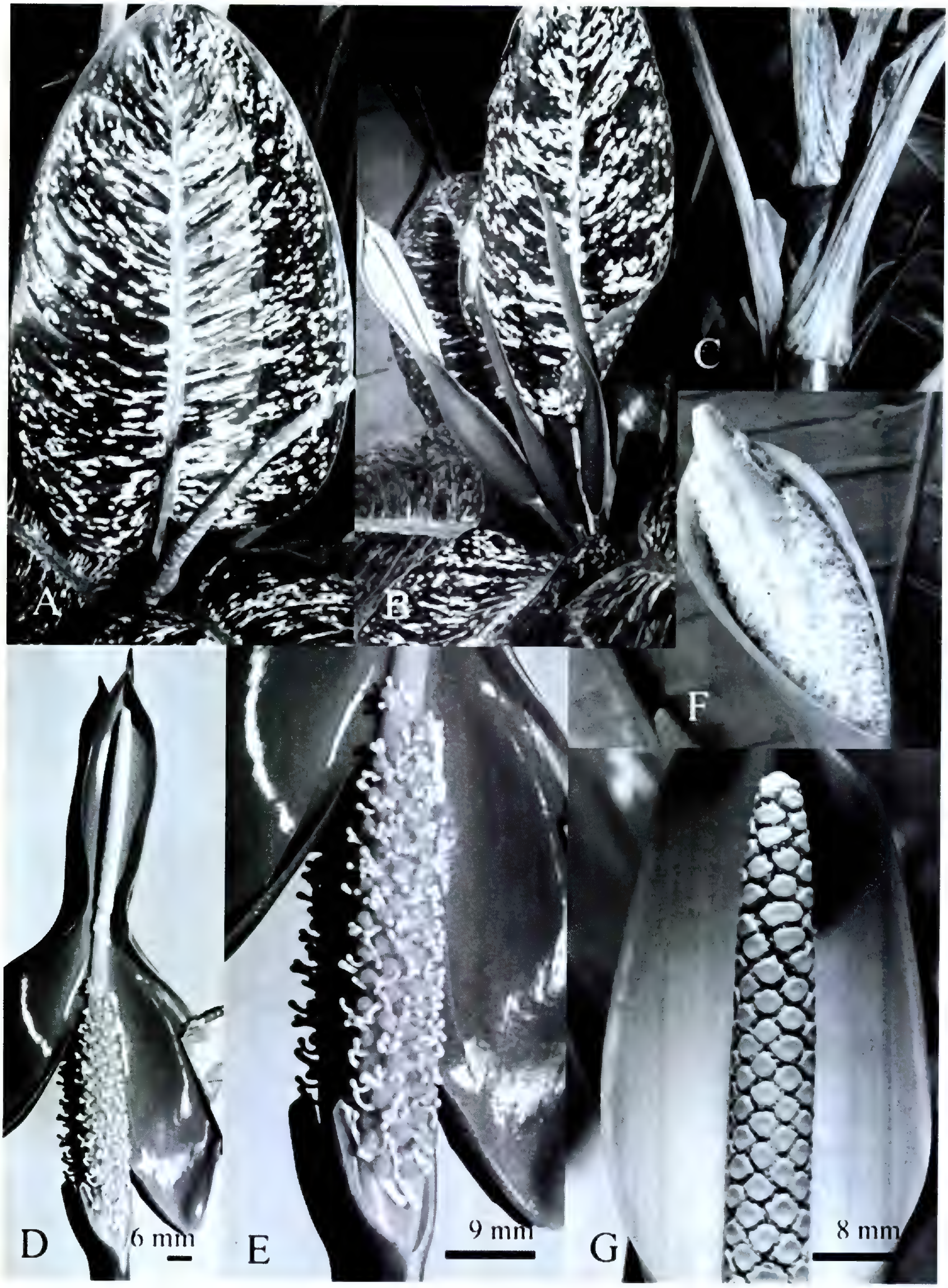


Figure 5. *Dieffenbachia concinna*. A–E, G. (*Croat 78318*). F. (*Croat 67594*). —A. Close-up of adaxial surface of blade. —B. Crown of plant with inflorescences, one open. —C. Close-up of stem and petiole bases showing variegations. —D. Close-up of opened inflorescence exposing entire spadix. —E. Close-up of inflorescence with portion of spadix showing elongated staminodia overtopping pistils. —F. Close-up of spathe showing emerging threads of pollen filling spathe. —G. Close-up of male portion of spadix showing androecia with anthers exposed.

size (to 1.3 m vs. 0.75–1 m in *D. oerstedii*), and more coriaceous blades typically broadest at the middle (vs. broadest below the middle in *D. oerstedii*) with more numerous primary lateral veins (6 to 12(14) vs. mostly 6 to 9 for *D. oerstedii*). In addition, the blades of *D. concinna* are glossy above and almost rounded at the base versus weakly glossy to matte and subcordate in *D. oerstedii*.

Grayum et al. 10588, from the headwaters of the Río Piedras Blancas in Puntarenas Province, is unusual not only in occurring much higher (to 900 m) than most collections of this species but in having a broader leaf (to 19 cm wide) with a longer petiole (to 30 cm). In other respects it agrees with other collections of *D. concinna*. *Hammel 9660*, collected at La Selva in Heredia Province in Costa Rica, probably represents a hybrid between *D. beachiana* and *D. concinna*. The specimen has the slightly scabrous petioles and the impressed major veins of *D. beachiana*, but the blades are more or less elliptic and dry more the color of *D. concinna*. *Croat & Hannon 79199*, collected south of Palmar Norte, appears to be a hybrid between *D. aurantiaca* and *D. concinna*. Its blade shape and maculations, and numerous inflorescences suggest *D. concinna*, while the broadly sulcate petiole favors *D. aurantiaca*.

Additional specimens examined. COSTA RICA. **Heredia:** near Puerto Viejo along rd. near Río Sucio, *Croat 35688* (MO), *Croat 35702* (MO); Finca La Selva, OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, *Hammel 9688* (DUKE), *Croat 78732* (INB, MO, W). **Limón:** La Colombiana Farm, United Fruit Co., *Standley 36739* (US); headwaters of Quebrada Mata de Limón, Finca Anai (Sixaola region), *Grayum et al. 4447* (MO); Cerro Tortuguero junto a la Barra de Tortuguero, *R. Robles 2090* (CR, INB, MO), *Barringer et al. 1973* (F); Par. Nac. Tortuguero, *Gómez-Laurito 7856* (CR); Boca de las Lagunas de Tortuguero, *Burger & Antonio 11249* (F, MO); Pococi, Refugio de Vida Silvestre Barra del Colorado, SE base of Cerro del Tortuguero, *Grayum et al. 11139* (CM, CR, INB, MO, USJ); Río Chirripócito-Río Sardina, Refugio Nac. Barra del Colorado, *Grayum 9777* (CR, MO); Río Reventazón, Finca Montecristo below Cairo, *Standley & Valerio 48960* (US). **Puntarenas:** *McAlpin 85-33* (SEL); 2 km NW of Chacarita, 30 km S of Palmar Sur, *Grayum & Fleming 8119* (CR, INB, MO); ridge betw. Río Riyito (valley of Laguna Chocuaco) & Quebrada Banegas, S of Cerro Rancho Quemado, *Grayum et al. 7567* (MO); Rincón de Osa Rancho Quemado, ca. 10 km W of main Rincón–Pto. Jimenez Rd., *Croat & Grayum 59785* (CR, MO); Osa, 6 km W of Rincón, *Grant & Rundell 92-01928* (CR, MO, US); near the airfield ca. 4 mi. W of Rincón de Osa, *Burger & Stolze 5461* (CR, F); Osa Península, NW of airfield, ca. 5 km W of Rincón de Osa, *Burger & Liesner 7196* (CR, F, MO, PMA); Osa Península, *Nicolson 3393* (BM, US); Costena-Cruces, Río Piedras Blancas, Cerro Anguciana, *Grayum et al. 10588* (INB, MO, CR); Río Sandalo, *Dodge 10198* (F, MO), *Dodge 10020* (F, MO); Palmar Norte de Osa, *Allen 5669* (EAP, UC, US); Osa Península, 4 mi. W of Rincón de Osa, *Raven 21532* (F); Rincón de Osa, Quebrada Aparicio-Quebrada Aguabuena, *Grayum et al. 3982* (CR, MO); vic. of Boscosa, at Quebrada Aguabuena, *Croat & D. Hannon 79238* (COL, INB, MO, NY, PMA, TEFH, TEX, UB); Sector Esquinas, vic. of Fila Gamba hills behind Esquinas Rain Forest Lodge, along Quebrada Negra, at end of side rd. off of Villa Bricena to Golfito Rd., *Croat & D. Hannon 79291* (CM, DUKE, INB, MO, P); Refugio Nac. Golfito, S tributary of Río Cañaza, *Grayum et al. 9250* (MO); W side Fila Gamba, ca. 6 km from Golfito airport, *Croat & Grayum 59930* (CM, K, MO); Río Claro, 2.5 mi. SE of Golfito, *Croat 67594* (MO); Orotina-Jaco, valley of Río Grande Tárcoles, 1 km S of Quebrada Ganado, vic. Hotel Pink Paradise, *Croat 79076* (INB, MO); Par. Nac. Corcovado, Monkey Woods, *Kernan & Phillips 831* (CR, MO); Lower Lookout Trail, *Kernan 748* (CR, MO); Est. Sirena, *Quesada 51* (INB, MO, US, CR); Península de Osa, Estación Biológica Los Patos, 8°34′N, 83°31′W, 200 m, 2 Sep. 1993, *R. Aguilar 2195* (CR, INB, MO); 0–1 km W of park headquarters at Sirena, *Liesner 2871* (CR, MO); Pan-Am Hwy., Rincón, *Croat & D. Hannon 79167* (MO); Rincón-Rancho Quemado, just S of Rincón near Río Rincón, *Croat & D. Hannon 79170* (HUA, INB, MEXU, MO, QCA, RSA, WU); vic. Palmar Norte, *Allen 5669A* (F, UC); Punta Banco, *M. Chavarría et al. 257* (CR); Coto Brus, Guaymí Reserve, river trail along Río Limóncito near jct. of Villa Palacios school trail, *Koshear 59* (CR); Golfito, Refugio de Vida Silvestre, *Marten 789* (CR); Carr. Inter-am.-Sinaí, Fila Huacas, ca. 4 km NE (by road) at Las Huacas ("Venecia"), *Grayum & Evans 10156* (CR, MO); Palmar Norte-Jalisco, Quebrada Benjamin, *Grayum et al. 9962* (CR, MO). **San José:** above Palmar Norte, *Croat 35108* (MO). NICARAGUA. **Río San Juan:** Res. Indio-Maíz, Caño el Tambor, branch of Río San Juan, *Rueda et al. 4070* (MO). PANAMA. **Panamá:** rd. to Puerto Jiménez, Osa, 40 km W of Panam. Hwy., rt. 2, *L. Gómez 19531* (MO).

Cultivated collections. Costa Rica. Puntarenas: Esquinas, 25 km SE of Palmar Sur, along Pan-Am Hwy., originally collected by Bruce McAlpin (Selby 85-33), 25 m, 2 Jan. 1994, cultivated at MBG, vouchered as *Croat 77281* (MO); 15 May 1996, *Croat 78318* (MO).

5. Dieffenbachia copensis Croat, sp. nov. TYPE: Panama. Coclé: El Copé, forest on Continental Divide above El Copé, 8°38′N, 80°38′W, 700–900 m, 27–29 Apr. 1985, *B. Hammel 13636* (holotype, MO-3284876!). Figures 6, 27B.

Herba 45 cm alta; internodia 7 mm longa, 7 mm diam., petiolus (17)21–29.5 cm longus, vagina 8–12.5 cm longa; pars libera 10.5–15.5 cm longa; lamina anguste oblanceolata, 25.5–33.3 cm longa, 5.2 cm lata; nervis primariis lateralibus 9–12 utroque; inflorescentia 1 per axillam; pedunculus 5 cm longus; spatha 15.7 cm longa, 1.2 cm lata; spadix 12.3 cm longus.

Small herb, to 45 cm tall; *internodes* about as long as broad, 7 mm diam., drying matte, dark brown, finely and irregularly folded; *petioles* (17)21–29.5 cm long, sheathed 41%–56% their length; sheath 8–12.5 cm long, narrowly acute at apex, drying dark brown to medium yellow-brown; free portion 10.5–15.5 cm long, subterete, obtusely sulcate, drying medium yellow-brown to dark

Figure 6. *Dieffenbachia copensis* (*Hammel 13636*). Type specimen.

brown, minutely granular to somewhat scabridulous; *blades* narrowly oblanceolate, 25.5–33.3 cm long, 5.2 cm wide, 6.4 times longer than wide, narrowly long-acuminate at apex, narrowly attenuate at base, dark green and matte above, moderately paler and semiglossy below, drying dark gray-green and minutely granular above, light yellowish gray below; *midrib* concolorous and narrowly raised above, convex and granular-puberulent to hispidulous and slightly darker below; *primary lateral veins* 9 to 12 pairs, arising at an acute angle then spreading at 45°–50° angle, prominently curved upward along the margins and extending to above the origin of the next higher veins, paler and weakly sunken above, convex and slightly darker below, drying narrowly raised and granular; minor lateral veins weakly visible; cross-veins equally visible on lower surface; lower surface moderately granular. INFLORESCENCE solitary, longer than the petioles; *peduncles* 5 cm long, drying 2.5 mm diam., pale yellow-brown; *spathe* 15.7 cm long, 1.2 cm diam., pale green, drying medium yellow-brown, narrowly long-acuminate at the apex (acumen 1.7 cm long); *spadix* 12.3 cm long; free portion 8.5 cm long; pistillate portion 5 cm long, 4–5 mm diam.; staminate portion 5.5 cm long, 4 mm diam., drying yellow-brown; mostly naked; intermediate sterile portion 1.1 cm long, 2.5 mm diam. on drying, with only a few staminodia scattered throughout its length; pistils 38, 2 to 3 situated across the width of the spadix; ovary 0.5–6.0 mm diam.; stigmas about as broad as the ovary; staminodia 2 to 4 per pistil, 1–1.4 mm long, slightly thickened toward the apex, not at all broadened toward the base; the sterile male flowers in 2 rows, somewhat separated from the fertile flowers; synandria 2.2–2.8 mm long, 1.6–2.0 mm wide, irregularly rounded to rhombic at apex. INFRUCTESCENCE not seen.

Distribution and habitat. *Dieffenbachia copensis* is known only from the type specimen in the Coclé Province of Panama at 700 to 900 m in the *Lower montane rain forest* (LM-rf) life zone (Holdridge, 1967).

Discussion. The species is characterized by its narrowly oblanceolate, narrowly long-acuminate blades with densely granular primary lateral veins and a granular-hispidulous midrib on the lower surface. The species is somewhat similar to both *D. galdamesiae* and *D. fortunensis*, differing from both in having proportionately narrower blades that are broader well above the middle. In contrast, the blades of *D. fortunensis* are broadest well below the middle and have the pistillate and staminate portions of the spadix contiguous or nearly so (vs. a free section to 1.1 cm long in *D. copensis*). *Dieffenbachia galdamesiae* differs in having blades proportionately broader, 2.7–4.2 times longer than wide, versus 6.4 times longer than wide in *D. copensis*.

6. Dieffenbachia crebripistillata Croat, sp. nov. TYPE: Panama. Coclé: Alto Calvario, above El Copé, ca. 6 km N of El Copé, Atlantic slope along trail which leads down to Las Ricas, Limón & San Juan, 8°39′N, 80°36′W, 710–800 m, 22 June 1988, *T. B. Croat 68746* (holotype, MO-3610884!; isotypes, B!, CAS!, COL!, DUKE!, F!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, PMA!, US!). Figures 7, 27A.

Planta 30–100(120) cm alta; internodia 2.5–4 cm longa, 1.5–3(5) cm diam.; petiolus 7.5–24 cm longus; lamina ovata vel raro elliptica vel oblongo-elliptica, (22)27–46(55) cm longa, 10–25 cm lata, nervis primariis lateralibus (10)15–17 utroque; inflorescentia 1–2 per axillam; pedunculus (8.5)10–14 cm longus; spatha 13–28 cm longa, 2.0–3.2 cm lata; spadix 13–26.5 cm longus; parte pistillata 6–10(12) cm longa, 8–12 mm lata.

Short, thick-stemmed herb, 30–100(120) cm tall; sap foul-smelling, eventually turning white; *internodes* dark green, glossy, 2.5–4 cm long, 1.5–3(5) cm diam.; *petioles* 7.5–24 cm long (averaging 16 cm long), somewhat spongy, solid dark green or with a white band on the abaxial surface, conspicuously sheathed ranging from 0.7 to fully throughout the length (but rarely ending more than 1 cm below the blade and often extending beyond the base of the blade); sheath to 1.5 cm high, 7.5–19.5 cm long, inequilaterally rounded to auriculate at apex; unsheathed portion usually not apparent but when present 1–7 cm long (averaging 1.6 cm long), broadly sulcate, the margins sharp; *blades* ovate to rarely elliptic or oblong-elliptic, (22)27–46(55) cm long, 10–25 cm wide (averaging 37 × 18 cm), 1.5–3.3 times longer than wide (averaging 1.9 times longer), 1.9–3.7 times longer than petioles (averaging 2.3 times longer than petiole), somewhat inequilateral, one side up to 0.5–2.7 cm wider, moderately coriaceous, abruptly acuminate and downturned at apex, obtuse to rounded at base, the basal portion of the blades held somewhat erect; upper surface glossy to moderately glossy, usually solid dark green sometimes mottled with pale green, slightly bicolorous; lower surface glossy, paler; *midrib* flat-raised to flat-rounded and paler especially near base, 12–20 mm wide, becoming obtusely convex toward apex and diminishing before reaching the apex above, broadly flat-rounded to narrowly rounded and pale green to white below (especially near the base); *primary lateral veins*

Figure 7. *Dieffenbachia crebripistillata* (*Croat 75172*). —A. Potted plant with open inflorescence (*Croat 75172*). —B. Close-up of crown of plant with open inflorescence. —C. Close-up of inflorescence with pollen emerging from androecia (*Croat 49243*). —D. Close-up of inflorescence with tube flared out and spathe blade recurved. —E. Close-up of inflorescence showing pistillate portion, intermediate sterile section, and lower section of staminate portion.

(10)15 to 17 per side, sunken to weakly sunken above, raised below; interprimary veins obscure above, obscurely visible below; minor veins moderately distinct on lower surface. INFLORESCENCES 1 to 2 per axil; *peduncle* (8.5)10–14 cm long, flattened laterally, pale green; *spathe* 13–28 cm long, 1.3–1.5 times longer than peduncle, pale to medium green outside (sometimes white at anthesis), paler within, unmarked, ± oblong, acuminate at apex, only weakly constricted midway (constricted area to 3.2 cm wide when flattened); spathe tube 1.5–3 cm wide when furled, 8–8.5 cm wide when flattened; spathe blade to 2.0–3.2 cm wide when furled; *spadix* 13–26.5 cm long (averaging 18 cm long), the free portion 8.5–11 cm long; pistillate portion 6–10(12) cm long, 8–12 mm wide; fertile staminate portion 5–9 cm long, 6–10 mm diam.; the mostly sterile intermediate portion (1)1.5–2.5 cm long, with some sterile male flowers in the upper ⅓; pistils (57)80 to 100, scattered, frequently adjacent, up to 5 in a row across the width of the spadix, never more than 5 mm apart; stigmas pale orange, densely pubescent; staminodia white, ± oblong, ca. 2–3 mm long, rounded at apex; synandria irregularly rounded at apex, smooth or weakly dimpled medially, to 2.6–2.8 mm diam.; pollen exserted in slender cream-colored threads to 3 mm long. INFRUCTESCENCES with *berries* ovoid to subellipsoid, orange to bright red, 8–11 mm long.

Distribution and habitat. *Dieffenbachia crebripistillata* is endemic to central and eastern Panama at (100)250–800(975) m, in *Tropical wet forest* (T-wf), *Premontane wet forest* (P-wf), and *Premontane rain forest* (P-rf) life zones (Holdridge, 1967) in Coclé, Colón, Panamá, and San Blas Provinces. While the species mostly occurs in a few areas of moderately high elevations (including Santa Rita Ridge, Cerro Bruja, Cerro Jefe, Cerro Campana, and La Mesa), it dips down to as little as 100 m along the Colón Province coast in the area of Río Guanche and Portobelo. Most of these collections differ in having petioles that dry less orange and have the petiole sheath ending somewhat below the blade, never overtopping the blades. As mentioned elsewhere under *D. nitidipetiolata* (and below) these collections may represent hybrids with either *D. nitidipetiolata* or *D. longispatha*.

Phenology. *Dieffenbachia crebripistillata* flowers principally at the end of the dry season (April) and in the early part of the rainy season from May to July, less commonly during the balance of the dry season (January–March) and in the latter part of the rainy season (August–October). Fruiting time is poorly known, but most fruiting collections have been made during the late rainy season (August–December).

Discussion. This species is related to *D. longispatha*, which differs in being a much more robust and taller plant (to 3.5 m), having petioles that dry green and with a long unsheathed portion, and pistils that are much larger (to 7 mm diam.), many fewer in number (only to 26), and widely spaced. See that species for additional discussion of the differences. Though *D. crebripistillata* usually has solid green blades, some plants from Coclé (at La Mesa near El Valle de Antón and along the Continental Divide north of Llano Grande) have pale-maculate leaves. Typically the petiole of *Dieffenbachia crebripistillata* is fully sheathed; however, some plants from the Cerro Jefe region (*Croat 35915*, *Croat & Zhu 76644*, and *Dwyer 9497*) or the Río Guanche region (*D'Arcy 9678* and *Croat 11420*) rarely have a significant free portion of the petiole 3–5(7) cm long.

Collections from lowland Colón (*Croat 75172*, *D'Arcy 9678*) are somewhat intermediate between *D. longispatha* and the more typical *D. crebripistillata* from the highlands of Panama. The petioles are not as fully sheathed, with the free portion of the petiole ranging from 4 to 5 cm long in these specimens.

Most collections from El Copé in Coclé Province have fully sheathed petioles and leaf blades proportionately smaller and narrower, averaging only 25 cm long (vs. an average of 37 cm for all other populations of the species) and 2.5 times longer than wide (vs. an average of 1.9 times longer) with petioles averaging only 11.5 cm longer (vs. an average of 16 cm for other populations). These collections (*Antonio 3039*; *Croat 44558*, *44682*, *49155*, *67576*; *Croat & Zhu 76757*; *Folsom 1265*, *3211*, *6218*; and *Sytsma & Andersson 4573*) differ in having smaller elliptic blades. The El Copé region is well known for having many endemics, and these plants may represent differences that may ultimately prove to be important, but for now are being considered as *D. crebripistillata*. One collection from El Copé in Coclé Province (*Croat 74861*) differs from the above only in having the petiole free above the sheath for a distance of 4.5 cm.

Etymology. The specific epithet is derived from "creber" (meaning crowded together) and "pistilla" (pistils) and refers to the very closely aggregated pistils on this species in contrast to the widely separated pistils of *D. longispatha* with which the species had long been confused.

Paratypes. PANAMA. **Coclé:** N of El Valle, Cerro Gaital, *Knapp 5758* (MO); El Valle de Antón Region, at La Mesa, 3.2–6 mi. above El Valle, *Luteyn & Kennedy*

1612 (DUKE), *FLORPAN, Guerra et al. 5252* (PMA), *Lewis et al. 1753* (MO), *Allen & Alston 1839* (MO); La Mesa, Finca Mandarinas, along rd. to Finca Furlong, *Croat 67115* (AAU, B, CAS, JAUM, M, MO, P, PMA, TEFH, VEN); 1 km E of Finca Macarenita, *Croat 7478* (MO); Divide SW of La Mesa, *Stein & Hamilton 990* (MO); La Mesa, above El Valle de Antón, ca. 2 km W of Cerro Pilón, *Croat 37361* (F, MO); above El Valle on rd. to Cerro Pilón, *Croat 25352* (MO); 2 km W of Cerro Pilón, *Sullivan 537* (MO); 3 km N of El Valle de Antón, *Wilbur et al. 15664* (DUKE); above El Valle, *Croat 13403* (MO); La Pintada–Coclecito, 5.3 mi. N of stream at Llano Grande, Atlantic slope, *Croat 49243* (HUA, MEXU, MO, PMA, SEL, VEN); rd. to Coclesito, 12 mi. from Llano Grande, *Churchill et al. 3993* (MO); past Llano Grande on rd. to Cascajal, *Sytsma et al. 4398* (MO); Llano Grande–Cascajal, *Hammel 7212* (MO); vic. Alto Calvario, 7 km N of El Copé, *Folsom 3211* (MO), *Folsom 6218* (MO), *Folsom 1265* (MO), *António 3039* (MO); above El Potroso sawmill, Cont. Divide, N of El Copé, *Sytsma & Andersson 4573* (MO); 9.4 km above El Copé, *Croat 44682* (MO), *Croat 44558* (MO); Alto Calvario, ca. 4.6 mi. above El Copé, *Croat 74861* (MO); Alto Calvario, 5.5 mi. N of El Copé, 3.5 mi. N of Escuela Barrigón, *Croat 67576* (MO, PMA), *Croat & Zhu 76757* (HUA, INB, K, MO, PMA, TEX), *Croat 49155* (MO, RSA, SCZ); Río Indio, on rd. from Portobelo to Nombre de Dios, *Croat 33568* (MO). **Colón:** ca. 5 mi. SW of Portobelo, *Croat 14175* (MO, PMA); 2 mi. S of Portobelo, *Croat 11420* (MO); S approach of Cerro Bruja from Río Escandaloso, *Hammel 3140* (MO); 9–12 mi. E of Trans-Isthmian Hwy. on Santa Rita ridge, *Thompson 4874* (CM, K, MO); Santa Rita Ridge, 26 km from Trans-Isthmian Hwy., *Knapp et al. 1717* (MO); Río Gatun, Portobelo, *Antonio 3820* (MO); Río Guanche, ca. 3–5 mi. above bridge inland, *Croat 26193* (MO), *D'Arcy 9678* (MO); ca. 3–5 km above bridge, *Croat 36958* (MO); ca. 3–5 mi. inland, *Croat 26239* (MO); Sabanitas-Portobelo, Río Piedras Lumber Rd, 6.7 mi. E of Sabanitas, 3.9 mi. up logging rd., *Croat 75172* (MO). **Panamá:** Par. Nac. Altos de Campana, Buena Vista, Chame, *FLORPAN, Espinosa et al. 4723* (MO, STRI), *Espinosa & E. Martínez 3308* (PMA); Sendero del Tigre, *Correa & Montenegro 10419* (PMA); trail to summit, *Correa & Montenegro 10647* (PMA); Cerro Campana, ca. 1 mi. from Interamerican Hwy., *Croat 35951* (F, MO, MY, PMA, QCA), *Croat 14707* (MO); along trail to summit, *Croat 17210* (MO, PMA, UB, VEN), *Croat 12123* (MO), *Croat 12086* (MO), *Croat 14789* (MO), *C. E. Smith Jr. & H. M. Smith 3389* (F), *Luteyn & Kennedy 1837* (DUKE), *Hammel 3781* (MO), *Luteyn 3188* (DUKE), *Croat 25213* (MO); Cerro Campana, 8.6 mi. SW of Capira, *Luteyn 1010* (DUKE); 6.1 mi. above Pan-American Hwy., *Croat 74760* (MO); 5–10 km NE of Altos de Pacora, *Mori & Kallunki 6026* (MO); rd. past Altos de Pacora, 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above Pan-Am Hwy., *Croat 68699* (MO); 0.8 mi. beyond turn-off to Altos de Pacora, *Croat & Zhu 76644* (MO); 4.6 km beyond peak on rd. to Altos de Pacora, 26.3 km from Interamerican Hwy., *Croat 35915* (MO); Cerro Jefe, *Dwyer & Gentry 9479* (DUKE, MO).

7. **Dieffenbachia davidsei** Croat & Grayum, sp. nov. TYPE: Costa Rica. Limón: headwaters of Quebrada Mata de Limón, central fork & hills betw. central & westernmost forks, Finca Anai (Sixaola region), 9°35′N, 82°39′W, 25–40 m, 19 Nov. 1984, *M. H. Grayum, G. Herrera, A. Matute & F. Chavarría 4483* (holotype, MO-3229671!; isotype, INB!). Figures 8, 27B.

Herba 30–100 cm alta; internodia (1.0)1.5–5 cm longa, 1.5–1.9 cm diam.; petiolus 3–11.5 cm longus, 5–6 mm diam., vaginatus 0.4–0.97 longitudinis, pars libera subteres vel D-formata, (1.5)2–5.5 cm longa; lamina oblongo-elliptica, 9–26.8 cm longa, 2.3–9 cm lata, nervis primariis lateralibus (6)9–15 utroque; inflorescentia 3 per axillam; pedunculus 1.5–4 cm longus; spatha 8–16 cm longa; spadix (7.5)10–12.5 cm longus; baccae 8–11 diam.; semina 2–3.

Slender herb, 30–100 cm tall; sap clear; *internodes* (1.0)1.5–5 cm long, 1.5–1.9 cm diam., weakly glossy to semiglossy, minutely roughened, usually with an even mixture of medium yellow-green and black-green streaks with no obvious background color, sometimes medium yellow-green toward base with black-green streaks, reversing to dark black-green with yellow-green streaks toward the apex, drying obviously minutely wrinkled, striate and matte. LEAVES spreading-pendent to pendent; *petioles* 3–11.5 cm long (averaging 6.5 cm long), 5–6 mm diam., arched-spreading from stem, sheathed from 0.4 to 0.97 (averaging 0.73) the length of the petiole, paler than stem, white to yellowish green speckled, especially near the base, the base often white, tinged with pink and dark-striate; sheaths auriculate-prolonged at apex (often appearing ± acute on dried specimens), the margins inrolled on both sides throughout their length, the opposite sides usually in contact and sometimes in part overlapping; unsheathed portion (1.5)2–5.5 cm long, subterete to D-shaped or broadly and obtusely sulcate, the margins moderately blunt; *blades* narrowly to broadly oblong-elliptic, 9–26.8 cm long, 2.3–9 cm wide (averaging 20.4 × 5.4 cm), broadest near the middle, (2)2.7–4.8 times longer than wide (averaging 36 times longer than wide), 1.9–6.2 times longer than petiole (averaging 3.1 times longer than petiole), slightly inequilateral, one side 3–9 mm wider than the other, sometimes weakly falcate, thinly coriaceous, gradually to abruptly long-acuminate at apex (acumen down-turned and apiculate), acute to rounded or cordulate and nearly equilateral or markedly inequilateral at base (one side sometimes also ending lower on the midrib); margins sometimes undulate; upper surface plain dark green in Costa Rica, sometimes variegated with irregular light green blotches in Panama populations, glossy to semiglossy; lower surface slightly paler, matte to weakly glossy; drying dark brown to dark gray-brown above, yellow-brown to yellow-green below; *midrib* flat at base, becoming weakly convex toward the apex, concolorous or paler

Figure 8. *Dieffenbachia davidsei*. —A. Potted plant showing habit with several inflorescences. —B. Blade adaxial surface with quilted primary lateral veins. —C. Close-up of stem showing mottled petiole and stems. —D. Crown of plant with cluster of inflorescences, and petiole showing free-ending sheath apex. —E. Abaxial surface of leaf blade and immature inflorescence. —F. Close-up of open inflorescence.

above, convex and paler than surface below, frequently pale-mottled; *primary lateral veins* (6)9 to 15 per side, flat to sunken, weakly quilted above, raised and darker than surface below, drying usually darker than surface below, sometimes paler than surface, usually departing midrib at 65°–90° angle throughout most of its length (rarely with the veins in the distal half of the blade arising at 30°–50°), prominently curved toward the apex in the outer ⅓, those near the base to as much as 120° angle, sometimes forming a weak sigmoid curve, the primary lateral veins in the upper ⅔ to ½ sometimes loop-connected for some distance, forming a weak collective vein 2–5 mm from margin, but this usually not extending all the way to the apex; interprimary veins almost as prominent as primary lateral veins, flat to sunken above, weakly raised and darker than surface below. INFLORESCENCES usually to 3 per axil, sometimes with more than one axil producing inflorescences; *peduncles* 1.5–4 cm long, 4–5 mm diam., ovoid to D-shaped in cross section; *spathe* 8–16 cm long, 3.1–4.8 times longer than peduncle, coriaceous, semiglossy on both surfaces, medium to light green outside, slightly paler within; tube oblong to somewhat ellipsoid, 6–7 cm long, oblong-lanceolate when opened, acute at apex (acumen apiculate for 2 mm); *spadix* (7.5)10–12.5 cm long, up to 1.7 cm shorter than the spathe; pistillate portion (4.0)5.5–6 cm long, (6)8–10 mm wide (the axis ca. 5 mm diam.), almost contiguous with the staminate portion (a wide sterile intermediate section lacking); the pistillate flowers more widely spaced near the apex, 4–6 mm apart; pistils 20–35, ovary globose, pale green; stigma bright yellow with long brushy papillae, 2–2.4 mm diam.; staminodia white, usually broadly united at base and forming an often nearly complete bowl around the pistil, somewhat flattened throughout, barely thickened at the apex, 3.4–5 mm long; staminate portion oblong, 4–6 cm long, creamy white, bluntly pointed at apex; synandria irregularly 4- to 6-lobed, drying 1.5–2.3 mm diam., deeply depressed with the margins turned up. INFRUCTESCENCES with spadix 5.5–7 cm long, *berries* orange, 8–11 mm diam., subglobose, 2- to 3-seeded.

Distribution and habitat. *Dieffenbachia davidsei* ranges from northeastern Costa Rica to Panama (Darién Province) and Colombia (Chocó) in *Premontane wet forest* (P-wf), *Tropical wet forest* (T-wf), and *Premontane rain forest* (P-rf) life zones (Holdridge, 1967). In Costa Rica it is known only from the Sixaola region at 20–40 m elevation. In Panama it ranges from 100 to 900 m in Panamá Province. The species frequently occurs in mature forest along streams.

Phenology. *Dieffenbachia davidsei* flowers in the rainy season sometime after May (one plant seen with both flower buds and seemingly mature inflorescences in late October). Mature fruits have been seen during the dry season, in the late rainy season, and early dry season from November through April. Immature fruits have been seen in late April indicating that flowering may begin even earlier than May.

Discussion. The species is distinguished by its slender, dark, semiglossy, mottled stems, mottled petioles with a prolonged, usually acute sheath apex, and more or less oblong blades with rather prominent primary lateral veins that spread at nearly 90°.

Dieffenbachia davidsei is probably most closely related to *D. obscurinervia*. That species differs in usually being a larger plant (to 1.5 m) with prominently scurfy brown internodes, petiole sheaths which are typically only rounded at the apex (not free-ending), and blades which have weakly developed primary lateral veins that arise at an angle, usually about 45° to the midrib.

Although the broadly spreading primary lateral veins are one of the most distinctive characteristics of *D. davidsei* (with the veins usually spreading from the midrib at a broad angle even to near the apex of the blade), a few collections from the El Llano–Cartí Road in Panama (especially the PMA sheet of *Paredes 940*) have primary lateral veins that spread at angles of up to 45°. The *Paredes 940* collection also has more conspicuously punctate petioles than does the MO sheet of the same number. It is possible that *Paredes 940* is a hybrid between *D. davidsei* and *D. obscurinervia*. Both species occur in the Nusigandí area along the El Llano–Cartí Road. *Dieffenbachia obscurinervia* also has conspicuously mottled petioles, but its veins arise at a much more acute angle. The stems of *D. obscurinervia* differ markedly in being matte and scurfy-brown rather than semiglossy, dark black-green with yellow-green mottling as in *D. davidsei*. Another unusual collection, possibly also a hybrid, is *Croat & Zhu 76666* from La Mesa in Coclé Province near El Valle de Antón. It has the glossy internodes of *D. davidsei* but the veins of *D. obscurinervia*. It is perhaps just an unusual collection of *D. obscurinervia*.

Etymology. The species was first collected in Panama by Scott Mori in 1974 along the El Llano–Cartí road (*Mori et al. 4184*), and later in Costa Rica by Gerrit Davidse and C. H. Hamilton (*Davidse & Hamilton 23617*) in 1983. It is named in

honor of Gerrit Davidse of the Missouri Botanical Garden, co-editor of the *Flora Mesoamericana* series.

Paratypes. COSTA RICA. **Limón:** Quebrada Mata de Limón, Finca Anai (Sixaola region), *Grayum et al. 4440* (CR, MO). PANAMA. **Bocas del Toro:** Fortuna Lake Area, Fortuna-Chiriquí Grande, 1.6 mi. N of Cont. Divide, *Croat & Zhu 76533* (MO). **Coclé:** Caño Blanco del Norte-Caño Sucio, *Davidse & Hamilton 23617* (MO, PMA); El Copé, Cont. Divide, *Hammel 13685* (MO); El Copé, ca. ½ mi. N of Cont. Divide at Alto Calvario, *Croat 75100* (MO); Atl. slope, *Hammel 5607* (MO). **Darién:** Par. Nac. del Darién, of Río Pucuro, vic. Tacarcuna, ca. 18 km E of Pucuro, *Hammel et al. 16397* (MO). **Panamá:** El Llano–Cartí Rd., 9.8 km from Interam. Hwy., *Mori et al. 4184* (MO). **San Blas:** trail to Cerro Camucañala from Río Titamibe, *de Nevers et al. 4709* (MO, PAN); Comarca de Kunayala, Nusigandí, El Llano–Cartí Rd., 10.1 mi. N of Interam. Hwy., Paseo Mariska, *Croat & Zhu 77017* (INB, MO); El Llano–Cartí Rd., *de Nevers & H. Herrera 3975* (MO); km 18, *Galdames et al. 1330* (STRI); Nusigandí, El Llano–Cartí Rd., betw. Nusigandí and 1 mi. N of Nusigandí, *Croat & Zhu 76597* (HUA, MO); Sede de Campo de PEMASKY, ca. 20 km on El Llano–Cartí Rd., *Paredes et al. 940* (MO, STRI); Isla Narganá, tributary of Río Diablo, *Galdames et al. 1570* (PMA, STRI). **Veraguas:** Cerro Tute, above Alto de Piedra, *McPherson 10725* (MO). COLOMBIA. **Chocó:** Nuquí, Corr. Arusí, Est. Biol. El Amargal, along trail to Arusí, *Croat & Mora 83685* (MO).

8. Dieffenbachia fortunensis Croat, sp. nov. TYPE: Panama. Chiriquí: along road between Fortuna Lake and Chiriquí Grande, 4.5–5 km N of dam of Fortuna Lake, 8°43′N, 82°17′W, 1100–1135 m, 8 Mar. 1985, *T. B. Croat & M. H. Grayum 60002* (holotype, MO-349012!; isotype, PMA!). Figures 9, 28A.

Herba 40–100 cm alta; internodia 1–5 cm longa, 0.8–2.0 cm diam.; petiolus 12–28 cm longus, vaginatus 0.37–0.83 longitudinis; vagina 6.5–14.5 cm longa, decurrens ad apicem; lamina oblongo-lanceolata, raro interdum anguste ovata vel anguste oblanceolata, 15–33 cm longa, 4.5–9.5 cm lata, nervis primariis lateralibus 10–17 utroque; inflorescentia solitaria; pedunculus 4.7–7 cm longus; spatha 12–18 cm longa; spadix 9–11.5 cm longus.

Slender herb, 40–100 cm tall; sap lacking distinctly foul aroma; stem erect except at base, containing inconspicuous, white raphide cells; *internodes* 1–5 cm long, 0.8–2 cm diam., unmarked, semiglossy, dark green to medium green, sometimes minutely wrinkled and glistening, drying blackened, moderately smooth (but minutely granular on magnification). LEAVES erect-spreading, ± clustered at/near stem apex; *petioles* 12–28 cm long (averaging 19.6 cm long), sheathing for 0.37–0.83 their length (averaging 0.58 their length); sheath 6.5–14.5 cm long (averaging 10.1 cm), with margins striate, decurrent distally, dark green, drying blackened to dark brown, surface matte, striate at base, minutely granular-roughened throughout with white raphide cells; unsheathed portion 3–15.5 cm long, sharply C-shaped, flat-sulcate, with margins prominently raised; *blades* narrowly oblong-lanceolate, rarely sometimes narrowly ovate, or narrowly oblanceolate, 15–33 cm long, (3.5)4.5–9.5(13) cm wide (averaging 21 × 6.8 cm) , 2–6.3 times longer than wide, 0.38–1.48 times longer than petiole (averaging 1.1 times longer), ± equilateral or weakly inequilateral, one side 5–15 mm wider than the other side, thinly coriaceous to subcoriaceous, drying papyraceous, usually quilted, weakly bicolorous, ± equilaterally or sometimes inequilaterally acuminate or sometimes acute at apex (acumen sometimes briefly apiculate), equilateral to slightly inequilateral and attenuate to acute, rarely rounded at base; margins usually conspicuously undulate, drying crisped; upper surface glossy to semiglossy or weakly glossy, medium to dark green, sometimes mottled white or cream; lower surface matte to weakly glossy, moderately paler; *midrib* flat or flat-raised and concolorous above, thicker than broad to convex below, drying brownish matte and darker than surface to slightly paler than surface, granular-puberulent to conspicuously granular below; *primary lateral veins* 10 to 17 per side, departing midrib at an acute angle, then moderately curved toward the margin at 55°–90° (mostly 55° in the middle of the blade but at more acute angles toward the apex and more obtuse angles toward the base), turning upward along the margins and forming a series of fine collective veins along the margins, some of which extend to the apex, matte, prominently sunken to narrowly or weakly sunken and concolorous above, thicker than broad or convex and darker than surface, granular-puberulent to conspicuously granular below, drying darker than surface; interprimary veins usually about as conspicuous as primary lateral veins; minor veins moderately obscure to distinct; "cross-veins" loose-connected, weakly oblique, drying minutely dark-punctate. INFLORESCENCES 1 per axil; *peduncle* 4.5–7 cm long; *spathe* 12–18 cm long, 2–3.7 longer than spadix, 1–1.5 cm diam. on tube when furled, gradually contracted midway, gradually long-tapered to apex, uniformly pale green on both surfaces; *spadix* 9–11.5 cm long, drying 3–3.2 mm diam.; free portion 1.5–2 cm long, drying 2 mm diam.; pistillate portion 4.2–6 cm long, drying 7 mm diam. throughout; fertile staminate portion 5–6.5 cm long, drying 4 mm diam. throughout; mostly naked intermediate portion of spadix 1.5–2.0 cm long, drying 2 mm diam., with a few sterile pistillate flowers in the lower half; pistils 35 to 38, well-spaced, rarely more than 2 dispersed across spadix width, de-

Figure 9. *Dieffenbachia fortunensis*. A, B. (*Croat 60002*). —A. Habit of sterile plant. —B. Leaf blade adaxial surface. C–F. (*Croat 76340*). —C. Leaf blade abaxial surface. —D. Stem showing petiole bases and free-ending sheath. —E. Close-up of stem showing acutely and broadly sulcate petiole. —F. Stem showing internodes and petiole bases.

pressed-globose, to 1.6 mm long, 1 mm diam., pale green; stigma yellow, about as broad as the pistil; staminodia white, 1–1.4 mm long, conspicuously thickened, drying pale orange-brown; the synandium 2–2.6 mm long, 1.6–2.0 mm wide, white, drying yellow-brown, the margins irregularly angular-subrounded. INFRUCTESCENCE with spadix to 6 cm long; *berries* not seen.

Distribution and habitat. *Dieffenbachia fortunensis* is apparently endemic to Panama, known only from the Fortuna Dam region of Chiriquí Province (hence the epithet) at 900 to 1600 m in *Premontane rain forest* (P-rf) and *Lower montane rain forest* (LM-rf) life zones (Holdridge, 1967).

Phenology. Flowering occurs during the late dry season and early wet season from March to June with fruits maturing in the late rainy season after September.

Discussion. It is distinguished by its usually small stature, moderately thin, prominently veiny, undulate, narrowly oblong-lanceolate to narrowly ovate blades with a flat-raised midrib, and petioles with the sheath decurrent at its apex and with a long, free, sharply flattened-sulcate distal portion. Also characteristic are the granular to granular-puberulent major veins on the lower blade surface.

The species is closest to *D. beachiana*, the latter differing in having the major veins on the lower surface conspicuously whitish puberulent and blades with primary lateral veins more numerous and spreading consistently at broader angles (most to ca. 90° throughout most of the blade rather than only a few veins near the base of the blade). In terms of pubescence *D. fortunensis* is closer to *D. galdamesiae*, which also shares granular puberulence rather than the loose puberulence of *D. beachiana*, but *D. galdamesiae* differs from *D. fortunensis* in having the primary lateral veins 15 to 17 per side and arising at a 30°–40° angle (vs. 10 to 17 per side, and at a 55°–90° angle). *Dieffenbachia galdamesiae* is also restricted to areas east of the Panama Canal, while *D. fortunensis* is restricted to far western Panama.

The species has been confused with small plants of *D. lutheri*, a similar species from Cerro Colorado in Chiriquí Province. That species usually has wider leaf blades (to 15 cm) that are ovate and dry less blackened. In addition, that species has the pistillate and staminate portions of the spadix contiguous, and lacks the mostly sterile section between the pistillate and staminate portion as is present on *D. fortunensis*.

Paratypes. PANAMA. **Bocas del Toro:** along Cont. Divide rd. N off main Fortuna–Chiriquí Grande Hwy., on mi. 1.1, *Croat & Grayum 60346* (MO). **Chiriquí:** Gualaca-Chiriquí Grande, 1 km S of Cont. Divide & Bocas del Toro boundary, *Croat 66866* (MO); 7.2 mi. beyond Los Planes de Hornito, *Croat 67837* (MO); 8.3 mi. NW of Los Planes de Hornito, *Croat 49971* (MO); rd. to Fortuna Dam site, N of Gualaca, 22.7 mi. beyond Río Estí bridge, *Croat 48672* (MO, PMA); 4.8 mi. beyond IRHE facilities at dam, *Croat 68012* (INB, MO, PMA), *Croat & Zhu 76340* (MO), *Thompson 4951* (CM, MO); Fortuna Dam area, Quebrada Los Chorros-Quebrada Hondo, to N of reservoir, *Churchill & Churchill 6158* (MO), *Churchill & Churchill 6159* (MO).

9. Dieffenbachia fosteri Croat, sp. nov. TYPE: Panama. Bocas del Toro: Laguna de Chiriquí, Nuri, 15 km E of Punta Cricamola, Ensenada de Catavela to Quebrada Nuri, 8°55′N, 81°49′W, elevation near sea level, 20 Mar. 1993, *R. Foster, A. Herre, E. Kalko & C. Handley 14649* (holotype, PMA!). Figure 27A.

Planta (0.4)1–2 m alta; internodia 1.5 cm longa, 1.5 cm diam. in sicco; petiolus 10–29 cm longus, vaginatus ⅓–½ longitudinis, pars libera subteres; lamina ovato-elliptica vel lanceolata vel anguste ovata, (14)17–28 cm longa, (6)7–14 cm lata, nervis primariis lateralibus 8–13 utroque; inflorescentia 1 per axillam; pedunculus 9.5 cm longus; spatha 20 cm longa, 2 cm diam.; spadix 18 cm longus; pars pistillata 6.5 cm longa (in fructu); baccae 6–7 mm diam in sicco, 1-loculares.

Slender herb, (0.4)1–2 m tall; sap smelling of oxalic acid; *internodes* medium green, dark green-mottled, 1.5 cm long, drying 1.5 cm diam. LEAVES clustered at/near stem apex; *petioles* 10–29 cm long, drying 2–3 mm diam., sheathing ⅓ to ½ their length; sheath margins drying ± hyaline and brown, sheath apex with one side obscure to rounded, with the other side acute; unsheathed portion of petiole subterete, oval in cross section, 12.5–18.5 cm from base of blade; *blades* ovate-elliptic to lanceolate or narrowly ovate, (14)17–28 × (6)7–14 cm, 2–2.4 times longer than wide, somewhat inequilateral, one side 1–1.5 cm wider than the other side, acuminate at apex, the acumen apiculate, 1 mm long, inequilateral and obtuse or rounded at base; *midrib* convex to flat-raised and concolorous above, drying somewhat flattened and concolorous above, convex and densely hispidulous, darker than surface below, drying striate with white inclusions below; *primary lateral veins* 8 to 13 per side, weakly sunken above, raised beneath, departing midrib at an acute angle then spreading at 65°–80° in the lower ½ of the blade, spreading at 45°–55° toward apex, extending almost straight toward the margins then broadly sweeping toward the apex; upper surface dark green, matte, drying dark brown to somewhat blackened; lower surface slightly paler than above, weakly glossy, drying slightly less grayish black than upper surface, densely grayish-speckled

below. INFLORESCENCES 1 per axil; *peduncle* 9.5 cm long, 5 mm diam.; *spathe* 20 cm long, 2 cm diam., gradually long-tapered, green throughout, the tube flattening to 3.5 cm wide; *spadix* 18 cm long, with pistillate portion to 6.5 cm long in fruit; *berries* 6–7 mm diam., dried, 1-locular.

Distribution and habitat. *Dieffenbachia fosteri* is only known from the type in western Panama near sea level in Bocas del Toro Province in the *Tropical moist forest* (T-mf) life zone (Holdridge, 1967).

Phenology. Little is known about the phenology of this species, but the type collection was in early fruit in March. Flowering probably occurred sometime during the rainy season.

Discussion. *Dieffenbachia fosteri* is characterized by its slender, rather weakly sheathed petioles and especially by its ovate-elliptic, somewhat blackish-drying blades. It is apparently not closely related to any other Central American species, though in the shape of blades and the decurrent sheath apex it is most similar to *D. killipii*. That species differs in having semiglossy blades that dry more or less green. It could possibly be confused with *D. grayumiana*, a species ranging along the Caribbean coast of Costa Rica to western Panama and probably occurring in the area where *D. fosteri* was collected; however, the latter differs from *D. fosteri* in having narrowly ovate-subcordate blades that are typically conspicuously pale-maculate and also in drying olive-green to yellowish brown rather than blackened.

Etymology. The species is named in honor of one of its collectors, Robin Foster, from the Field Museum of Natural History in Chicago, an expert on Neotropical plant ecology and the vegetation of the Neotropics.

10. Dieffenbachia galdamesiae Croat, sp. nov. TYPE: Panama. Comarca de San Blas: Pemasky, Sendero Nergan Igar, km 15 on El Llano–Cartí Road, 9°20′N, 78°58′W, 350 m, 2 July 1994, *C. Galdames, T. B. Croat & M. Alba 1222* (holotype, MO-5548504!; isotypes, AAU!, B!, COL!, F!, GH!, INB!, K!, MEXU!, NY!, PMA!, RSA!, S!, SCZ!, UB!, US!, VEN!). Figures 10, 28A.

Planta 50–80 cm alta; internodia 6–20 mm longa, 0.5–2.0(3.0) mm diam.; petiolus 18–43 cm longus, C-formatus, vaginatus 0.25–0.66 longitudinis; lamina oblongo-elliptica, 27–60 cm longa, 6.7–18 cm lata, nervis primariis lateralibus 15–17 utroque; inflorescentia 3 per axillam; pedunculus 5.5–15 cm longus; spatha 14–25 cm longa, 2 cm diam.; spadix 15.7–18 cm longa; pars pistillata 7.3–10 cm longa, 8 mm diam.

Small herb, to 50–80 cm tall; sap lacking foul odor but weakly caustic to skin; stem supported at base by adventitious roots; *internodes* 6–20 × 0.5–2.0(3.0) mm diam., dark green, weakly to moderately glossy; petiole scar oblique, one side 3–4 mm wider than the other; *petioles* 18–43 cm long (averaging 29 cm long), densely granular-puberulent, sheathed 0.25–0.66 their length (averaging 0.43 their length); sheath erect to involute, 6.5–20 cm long (averaging 12.3 cm long), inequilaterally rounded to acute at apex; unsheathed portion 10–25 cm long (averaging 16.5 cm long), sharply C-shaped, broadly concave adaxially; *blades* oblong-elliptic, 27–60 cm long, 6.7–18 cm wide (averaging 40.8 × 11.7 cm), 2.7–4.2 times longer than wide (averaging 3.6 times longer), 1.1–1.8 times longer than petioles (averaging 1.2 times longer than petioles), acuminate at apex, acute at base, inequilateral, one side to 1.5 cm wider than the other, thinly coriaceous, drying moderately thin; upper surface dark green and semiglossy, drying dark brown to olive-green; lower surface slightly paler, almost matte, drying weakly glossy, grayish to yellowish brown; *midrib* broadly convex-flattened and concolorous above, narrowly rounded, matte, darker and sparsely granular-puberulent below, drying darker than surface, flattened to ridged with one or both margins narrowly raised; *primary lateral veins* 15 to 17 per side, arising at 30°–40° angle, sweeping prominently toward the apex with as many as 4 to 5 of them simultaneously coursing along the margin within 1 cm of the margin, sometimes forming weak collective veins, weakly quilted-sunken above, convex and sparsely granular-puberulent and somewhat scurfy below, drying darker than surface with the center collapsed and the margins often thin and upturned; minor veins obscurely to moderately visible and darker than surface above, drying moderately distinct; cross-veins sometimes drying moderately distinct below. INFLORESCENCES to 3 per axil; *peduncle* 5.5–15 cm long, 5–8 mm diam., drying 2.5–5 mm diam.; *spathe* 14–25 cm long, 1.6–2.5 times longer than peduncle, 2 cm diam. at tube, green on both surfaces; *spadix* 15.7–18 cm long; free portion 9.5–12 cm long; pistillate portion of spadix 7.3–10 cm long, 8 mm diam.; staminate portion of spadix 7–8.5 cm long, 6 mm diam.; the mostly sterile intermediate portion 1.3–2.5 cm long with a few pistillodes extending in the lower ½; pistils 59 to 68, moderately closely spaced, 2 to 4 situated across the width of the pistils; ovaries 1.2–2.0 mm diam.; stigmas 1.6–2.2 diam., depressed-globose; staminodia club-shaped, 1.8–2.8 mm long, 0.4–1.0 mm wide, flattened, free to base, not expanded toward the base, thickened

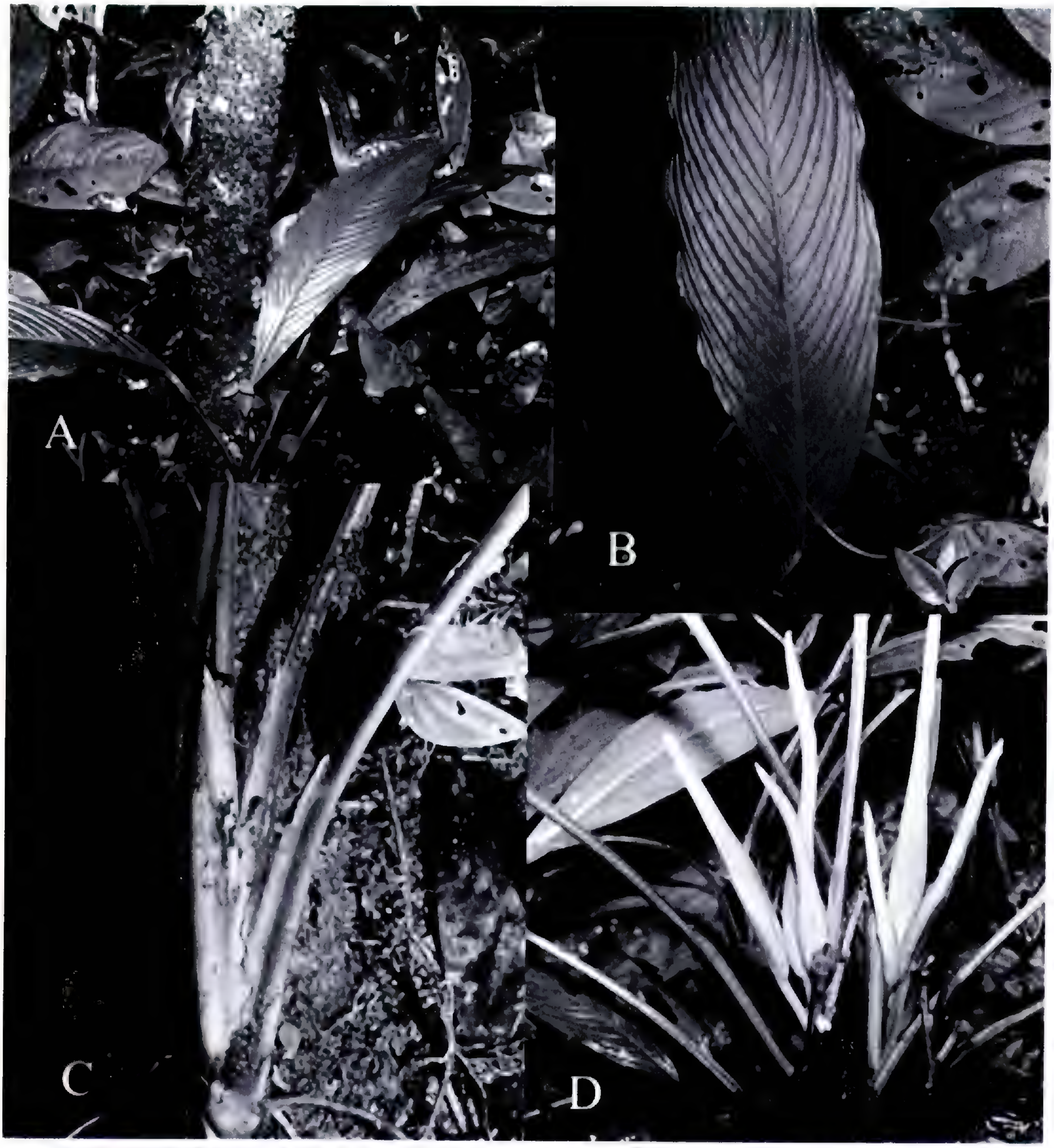


Figure 10. *Dieffenbachia galdamesiae* (*Croat 76560*). —A. Habit. —B. Leaf blade adaxial surface. —C. Close-up of stem showing roots and petiole bases. —D. Petioles and clusters of inflorescences.

and somewhat granular-puberulent at apex; synandria 2.4–2.8 mm diam., irregularly rounded, broadly sulcate to truncate with slightly overlapping edges, the margins ± crenulate. INFRUCTESCENCES not seen.

Distribution and habitat. *Dieffenbachia galdamesiae* is endemic to Panama, known only from central Panama on both sides of the isthmus in the *Tropical wet forest* (T-wf) life zone (Holdridge, 1967) at 350 to 500 m elevation. It occurs in swampy conditions in creek beds in virgin forest in nearly full shade.

Phenology. The species has been seen in flower in June as well as in October. Mature fruits have been seen in December.

Discussion. The species is characterized by its moderately small habit, only to 80 cm tall, the granular-puberulent petioles and major veins on the lower blade surface. It is most closely related to *D. beachiana* and *D. fortunensis*, differing from both in having the primary lateral veins ascending at less than a 50° angle. It may prove to be only subspecifically distinct from *D. fortunensis*.

Etymology. The species is named in honor of

Chilean botanist Carmen Galdames, a long-time resident of Panama, who has collected in Panama for the SCZ herbarium at the Smithsonian Tropical Research Institute. Carmen was the first to bring the species to my attention and also collected the type specimen.

Paratypes. PANAMA. **Panamá:** El Llano–Cartí Rd., 6.8 mi. from hwy., *Croat 49124* (MO). **San Blas:** Comarca de Kunayala, Nusigandí, El Llano–Cartí Rd., 9 mi. N of main hwy., Nergan Igar (Nergan Trail), *Croat & Zhu 76560* (MO, PMA). **Veraguas:** Dos Bocas del Río Calovéborita, 16–17 km NW of Santa Fe, *Dressler 5316* (MO).

11. Dieffenbachia grayumiana Croat, Novon 9: 494. 1999. TYPE: Costa Rica. Limón: Refugio Nacional Barra del Colorado, forests and pastures between Río Chirripócito and Río Sardina [Sardinal], 10°8′N, 83°5′W, 12 m, *M. H. Grayum 9773* (holotype, MO-4370212!; isotype, INB!). Figures 11, 27A.

Stout herb, 1–1.5 m tall; stems erect at apical part, the older portion reclining for up to 1.5 m; *internodes* 2.5–8.5 cm long, 2–3.5(–10) cm diam., dark green, glossy, variegated with cream-yellow or pale green (sometimes medium green with dark green lines as in *Croat & Grayum 60149*); *petioles* (24–)30–59 cm long (averaging 39 cm long), sheathed from 0.3 to 0.55 their length (averaging 0.42), matte, dark olive-green to deep brown, streaked or tinged with cream-white in lower half, especially near the base, subterete; sheath 19–29 cm long, usually decurrent at apex, sometimes weakly free-ending (as in *Croat & Grayum 60149*); unsheathed portion 13–28.5 cm long, weakly sulcate adaxially, weakly flattened toward the apex, sometimes slightly white adaxially and continuing white onto lower midrib; *blades* narrowly ovate to oblong-ovate, (22)30–54 × 10–32 cm (averaging 36 × 18 cm), 1.5–2.6 times longer than wide (averaging 1.9), ranging from 0.6 as long as petioles to 1.4 times longer than petioles, but averaging about as long as petioles, slightly inequilateral, one side 1–1.5 cm wider than the other, acuminate to abruptly acuminate at apex, inequilaterally subcordate (sinus to 3.5 cm deep) or rarely inequilaterally rounded at base (sometimes one side weakly subcordate, the other side rounded), subcoriaceous, drying thin, slightly concolorous to slightly bicolorous; upper surface usually glossy to semiglossy, dark green, to weakly mottled cream, drying dark olive-green, plain (unvariegated) to usually conspicuously mottled yellow-cream; lower surface semiglossy to nearly matte, slightly paler, drying yellowish green; *midrib* flat to weakly flat-raised or broadly convex (sometimes broadly sunken at base, broadly flat-raised and striate toward apex) slightly paler and dark green-spotted to concolorous above, convex to narrowly rounded and white or narrowly acute and paler below; *primary lateral veins* 13 to 18(to 22) per side, gradually arising at a steep angle from the midrib, then spreading in a broad curve at 55°–80° angle, (those near the apex to 25° angle, those near the base sometimes 90°–110° angle and sometimes forming a sigmoid curve), deeply sunken above, convex below, forming a series of weakly developed collective veins that eventually merge with the margin; at least the midrib and primary lateral veins sometimes minutely farinose-granular; minor veins moderately obscure below. INFLORESCENCE 1 to 3 per axil, sometimes subtended by a reduced leaf with a fully sheathed petiole (the sheath emarginate at apex) and a reduced leaf blade, 12–15 × 3.5–6.5 cm; *peduncle* 8–12 cm long, drying 2–3 mm diam.; *spathe* 16.5–23.5 cm long, 3–4 cm longer than the spadix, 4.0–5.0 cm wide at base, to 2.5–3.5 cm wide at constriction, 2.5–3 cm wide on blade (to 7 cm wide when flattened), uniformly light green to medium green on both surfaces, weakly glossy throughout outside, somewhat glossier within; *spadix* 15–27 cm long; free portion 7–13 cm long; pistillate portion 8.0–9.3 cm long, drying 7–10 mm wide; staminate portion 5–6.5 cm long, white, tapered toward apex and tapered slightly toward the base; the staminate and pistillate portions separated by an almost sterile intermediate segment 2–2.5 cm long with a few scattered pistils in the lower half and a few scattered staminodia in upper half; pistils 115 to 160, densely aggregated, separated from one another by 0.5 to 2.5 times their width, irregularly scattered with roughly 4 to 5 covering the width of the spadix; ovaries pale lemon-yellow, depressed-globose, 1.8–2 mm wide; staminodia white, 3 to 5 per pistil, free or briefly united at base, 1.5–2.2 mm long; synandria 1.2–1.6 mm diam., irregularly angled with rounded margins. INFRUCTESCENCES to 27 cm long, with fruiting portion 10–14 cm long; *berries* red-orange, subglobose, ovoid to ellipsoid, 5–7 mm diam.

Distribution and habitat. Dieffenbachia grayumiana ranges along the Atlantic slope from northwestern Costa Rica to western Panama, mostly near sea level but ranging up to 1300 m in Costa Rica in Alajuela Province (vic. of Monteverde Reserve) and to 480 m in Heredia Province. Grayum (pers. comm.) reports the species to occur mostly in light gaps and disturbed areas in primary forest at the La Selva Reserve in Costa Rica.

Phenology. Flowering occurs in *D. grayumiana*

Figure 11. *Dieffenbachia gravumiana*. —A. Habit (*Croat 60149*). B–D. (*Croat 74953*). —B. Leaf blade adaxial surface. —C. Blade abaxial surface. —D. Apex of stem showing heavily sheathed petioles with sharply sulcate free portion, and speckled petiole bases.

from January to June, rarely as early as November. Fruiting collections have been seen only from May to September.

Discussion. The species is characterized by its narrowly ovate, typically subcordate, mottled blades; weakly sheathed, decurrent petioles; and variegated stems and petioles. Also characteristic are blades that are frequently glossy on the upper surface and matte or nearly so on the lower surface. The major veins are sometimes minutely farinose-granular on the lower surface. In this regard it is similar to *D. beachiana*, a species with puberulent major veins on the lower blade surface. Aside from pubescence type, *D. beachiana* also differs in having much narrower blades (1.8–5.3 times longer than wide) with more numerous pairs of primary lateral veins (23 to 36 pairs).

Dieffenbachia grayumiana is superficially similar to *D. seguine* from the West Indies in the shape and coloration of its dried blades but lacks the sharply sulcate petioles, the bicarpellate ovaries, and the protruding stubby spadix with a reflexed spathe blade seen in the latter.

A collection from Bocas del Toro Province in Panama (*Croat 74945*) differs in having larger concolorous blades (54 × 30 cm) that are only weakly glossy on the upper surface, with only weakly sunken primary lateral veins. Another collection from Bocas del Toro, *Croat & Grayum 60149*, had stems to ca. 10 cm diam., substantially larger than those of any other collection reported.

Additional specimens examined. COSTA RICA. **Alajuela:** Puntarenas-Guanacaste, Peñas Blancas, *Dryer 1681* (F); Río Peñas Blancas, *Burger et al. 10734* (CR, F); Upala, Río Zapote, 5 km S of Canalete, *Burger & Baker 9968* (CR, F). **Heredia:** Río Sarapiquí, La Virgen, 1974, *Horich s.n.* (M); La Zona Protectora, Río Peje-Río Guacimo, *Grayum & Schatz 3206* (DUKE); Secondino's woods, off Occidental, *Kress 84-1632* (SEL); Río Peje-Río Sardinalito, Atl. slope of Volcán Barva, *Grayum 6887* (MO); San José, Pto. Viejo, vic. of Chilamante, 11.6 mi. N of Cariblanco, *Croat 68359* (B, CR, M, MO); La Selva, *Croat 78733* (COL, INB, MO, NY, SEL); upstream on Río Puerto Viejo, *Burger & Matta 4181* (CR, F); OTS Field Station along Río Puerto Viejo just E of jct. with Río Sarapiquí, *Beach 1440* (DUKE), *Beach 1441* (DUKE), *Chacón 507* (DUKE), *Croat 44321* (MO), *Folsom 9724* (MO), *Hammel 8167* (MO), *Hammel 8873* (DUKE), *Grayum 2288* (DUKE). **Limón:** Ref. Gandoca-Manzanillo, Río Gandocaca, *Grayum et al. 8038* (CR, MO); 3.5 air km S of Islas Buena Vista in the Río Colorado, 16 km SW of Barra del Colorado, *Davidse & Herrera 31213* (INB, MO); Cerro Coronel, E of Laguna Danto, *Stevens 23642* (CR, MEXU, MO); Río Chirripócito–Río Sardina, Ref. Nac. Barra del Colorado, Río Chirripócito–Río Sardina, *Grayum 9830* (MO); Guacimo-Guapiles Rd., *Barringer 2432* (F); Pococi, Par. Nac. Tortuguero, Río Suerte betw. Río Palacio–Caño Penitencia, *Grayum et al. 11116* (INB, MO); Lomas de Sierpe, S from Río Tortuguero, *Grayum et al. 11163* (INB, MO). PANAMA. **Bocas del Toro:** Almirante-Bocas del Toro, near Milla 5, *Croat & Porter 16499* (MO); Chiriquí Grande-Fortuna, 3 mi. W of Chiriquí Grande, *Croat & Grayum 60149* (K, MO, PMA, US); Gualaca-Chiriquí Grande, 8.1 mi. S of Punta Peña, *Croat 74953* (MO, PMA). **Chiriquí:** Gualaca-Chiriquí Grande, 1.4 mi. S of Punta Peña, *Croat 74945* (MO), *M. Akers 78A* (MO).

12. Dieffenbachia hammelii Croat & Grayum, Novon 9: 496. 1999. TYPE: Costa Rica. Heredia: Finca La Selva, O.T.S. Field Station on the Río Sarapiquí, 50–80 m, *M. H. Grayum 7670* (holotype, MO-3491533!; isotypes, B!, CR!, K!). Figures 12, 27B.

Small herb, 25–40(70) cm tall; sap not foul-smelling; stem becoming decumbent and subrhizomatous at base; internodes 1–1.5(2.7) cm long, on lower portions, 3.5–7.5 cm long toward the apex, 0.5–2 cm diam., glossy, dark blackish green, drying yellowish brown to gray-green, weakly striate. LEAVES erect-arching; *petioles* 7–25(35) cm long (averaging 15 cm long), erect, green or mottled with dull yellow-green, drying greenish to sometimes yellowish brown, surface drying matte, sheathing for (0.3)0.4–0.8 the petiole length (averaging 0.63 their length), sheath 5.5–13 cm long (averaging 8 cm); unsheathed portion 1–9 cm long, rarely to 15 cm long, narrowly C-shaped to D-shaped in cross section, narrowly sulcate adaxially, with margins finely acute, the tip narrowly decurrent, sometimes difficult to discern where it ends; *blades* narrowly to broadly elliptic or oblanceolate, 9–28 × 3.2–13(15) cm (averaging 19.5 × 7.5 cm), 1.7–3.4 times longer than wide (averaging 2.7 times longer than wide), 1.1–1.5 times longer than the petiole; equilateral to slightly inequilateral, one side 0.5–1 cm wider than the other (the narrower side usually plane, the wider side usually minutely undulate), weakly to semiglossy, acuminate, narrowly to broadly acute or attenuate at apex, and equilateral or slightly inequilateral, rarely obtuse at base, thinly coriaceous, slightly to moderately bicolorous; upper surface medium to dark green, weakly glossy to semiglossy, drying light yellow-green to dark brown; lower surface weakly glossy to matte, slightly to moderately paler, drying yellow-green, sometimes yellow-brown; *midrib* flat-raised, rarely convex (sometimes obscurely sulcate medially), 1–3 mm diam., slightly paler than surface above, convex to narrowly convex below, drying pale brown, matte, with short, white raphide cells; *primary lateral veins* 9 to 17 per side, departing midrib at a 40°–50° angle, weakly curved to the margins, weakly sunken or slightly raised in weak valleys, weakly quilted and concolorous above, convex and weakly pleated-raised, drying moderately inconspicuous, slightly

Figure 12. *Dieffenbachia hammelii*. A, E. (*Croat 78738*). —A. Habit of plant in the wild. —B. Potted flowering plant showing habit (*Duke 81-157*). —C. Potted plant with inflorescence at anthesis (*Croat 78731*). D, F. (*Croat 78731*). —D. Leaf bases and cluster of inflorescences, the one on the right at anthesis. —E. Crown of plant with an open inflorescence. —F. Crown of plant with a cluster of inflorescences (one cut away to expose full-sized berries).

darker than surface or slightly paler than surface below; the interprimary veins almost as conspicuous as primary lateral veins; minor veins darker than surface below, drying moderately faint; "cross-veins" darker than surface below, drying moderately faint. INFLORESCENCES 1 to 3 per axil; *peduncle* 4.5–11 cm long, subterete in cross section; *spathe* (8)10–16 cm long, 1.3–2.7 times longer than peduncle, medium green throughout, and weakly glossy outside, medium green and glossy inside, cuspidate to acuminate at apex; spathe tube 6.5–12.5 cm long, 1.2–2.3 cm diam., free portion 3–6 cm wide when flattened; *spadix* 6.5–15.5 cm long; free portion 4.7–7.5 cm long; pistillate portion 5–8.5 cm long, 6–7 mm diam. throughout, fused with spathe for up to 4 cm; fertile staminate portion tapered to both ends, moderately acute at apex, (1.7)3–4.5 cm long, 6–7 mm diam. throughout; sterile intermediate segment (0.8)2–3 cm long, with a few scattered staminodia throughout; pistils 26 to 43, ovoid, sparse to moderately dense, loosely scattered in clusters of 2 to 4 with up to 3 across the width of spadix but often with spaces between the groups of pistils up to twice the width of the spadix, sometimes in a spiral with up to 5 to 6 pistils; ovaries 1-locular, 2.4 mm long, 2.4 mm diam.; stigmas 1.6–1.8 mm diam.; staminodia 2.8–3 mm long, up to twice as long as pistils, free from one another at base, thickened at both ends, white at apex, but often translucent midway and drying flattened and very thin; synandrium bluntly 4- to 5-sided, margins irregularly shaped toward the base, ± rounded at apex, 2–2.5 mm diam. INFRUCTESCENCE with spathe pale orange outside; spadix 22 cm long; *berries* orange to bright red, obovoid-ellipsoid, 1 cm long, 8 mm diam.

Distribution and habitat. *Dieffenbachia hammelii* occurs in southeastern Nicaragua (Dpto. Río San Juan) and northern Costa Rica from sea level to 100 m in the *Tropical wet forest* (T-wf) life zone (Holdridge, 1967), in wet forests and swampy areas on the Atlantic slope.

Phenology. Flowering plants of *D. hammelii* have been seen from March through May and also July, while mature fruits have been seen in August and September. Cultivated plants at the Missouri Botanical Garden flowered in mid July and mid October.

Discussion. The species is characterized by its small stature, typically 25–40 cm; its glossy, decumbent, subrhizomatous stems; weakly sheathed, matte-drying petioles (sheath decurrent at apex); and moderately small, more or less oblong-elliptic, weakly inequilateral green leaf blades with moderately numerous primary lateral veins. One blade margin is usually plane and one margin usually minutely undulate.

In Costa Rica it is most easily confused with *D. oerstedii* or small plants of *D. grayumiana*, both of which can be distinguished in having the petiolar sheath auriculate at the apex rather than decurrent as in *D. hammelii*. At La Selva, where the species was first studied, *D. hammelii* is uncommon. One collection (*Hammel 8784*) reported that the sap was not foul smelling, as is the case with many species.

Additional specimens seen. COSTA RICA. **Heredia:** Finca La Selva, OTS Field Station on the Río Puerto Viejo, *Grayum 2772* (DUKE, MO). **Limón:** Tortuguero, near Boca de las Lagunas de Tortuguero, *Burger & Antonio 11224* (CR, F); Cerro Coronel, E of Río Zapote, 1 km from banks of Río Colorado, *Stevens 24257* (CR, MO); 2 air km SSE of Islas Buena Vista in the Río Colorado, *Davidse & Herrera 31077* (CR, MO); 3.5 air km S of Islas Buena Vista in the Río Colorado, *Davidse & Herrera 31154* (MO); Ref. Barra del Colorado [Sardinal], *Grayum et al. 9744* (CR, MO); Pococi, Tortuguero, N end of Lomas de Sierpe, S from Río Tortuguero, *Grayum et al. 11169* (CR, INB, MO). **San José:** Vazquez de Coronado, Braulio Carrillo NP, along San José to Siquirres Hwy., along trail to Río Sucio, Old Carillo Station site, *Croat 78758* (COL, GOET, INB, MEXU, MO, PMA, TEFH, UB, WU). NICARAGUA. **Río San Juan:** near Caño Chontaleno, 20 km NE of El Castillo, *Neill & Vincelli 3484* (MO); "Marcelo" near Río Sabalos, *Salick 8092* (MO).

13. **Dieffenbachia horichii** Croat & Grayum, sp. nov. TYPE: Costa Rica. San José: Cantón Pérez Zeledon, along road betw. San Isidro General–Dominical, Fila Tinamastes, 9°18′24″N, 83°46′11″W, 900–1100 m, *T. B. Croat & D. Hannon 79115* (holotype, MO-05095465!; isotypes, AAU!, B!, CAS!, COL!, CR!, DUKE!, F!, GH!, HUA!, INB!, K!, MEXU!, NY!, P!, PMA!, QCNE!, RSA!, S!, SCZ!, TEFH!, TEX!, UB!, US!, VEN!, WU!). Figures 13, 27A.

Planta terrestris, 1.0–1.5(2) m; internodia 1–3 cm longa, 4–6 cm diam.; petiolus 8–33 cm longus, vaginatus fere omnino; vagina libera 1.5 cm longa; lamina elliptica vel ovato-elliptica, 26–60 cm longa, 9–30 cm lata, nervis primariis lateralibus 14–21 utroque; inflorescentia 3–6 in quoque axilla; pedunculus 8.5–19 cm longus; spatha 14.5–32.5 cm longa; spadix 13–17 cm longus; pistilla 43–69.

Stout herb, 1–1.5(2) m tall; sap white, copious, foetid, caustic; stem erect on younger parts, to 1.2 m long and reclining on older parts, *internodes* 1–3 cm long, 4–6 cm diam., semiglossy to glossy, dark green to medium green; *petioles* 8–33 cm long (averaging 18.7 cm long), weakly glossy, sheathing nearly or completely throughout; sheath medium green streaked with yellow-green, margins involute, the tip free-ending and inequilaterally rounded-au-

Figure 13. *Dieffenbachia horichii*. A, B. (*Croat & Hannon 79115*). —A. Habit of flowering plant. —B. Crown of plant with cluster of inflorescences. C, D, E. (*Croat 79073*). —C. Plant with inflorescence at anthesis. —D. Close-up of stem with petiole bases. —E. Close-up of lamina base and close-up of inflorescence.

riculate (auricle sometimes extending up to 1.5 cm beyond blade); unsheathed portion lacking or to 1.2 cm long (rarely to 6 cm long), obtusely somewhat flattened in cross section; *blades* narrowly to broadly elliptic to ovate-elliptic, 26–60 × 9–30 cm (averaging 45 × 19 cm), 1.9–3.4 times longer than wide (averaging 2.5 times longer), 1.7–4 times longer than petiole, slightly inequilateral, one side 0.5–1.2 cm wider than the other side, subcoriaceous to coriaceous, somewhat bicolorous, acuminate at apex, ± equilateral and obtuse to rounded (rarely acute or narrowly rounded) at base, margins weakly undulate; upper surface dark green, semiglossy to highly glossy, drying dark gray-green to dark yellow-brown; lower surface weakly glossy to matte, moderately paler, drying yellow-brown to yellowish green; *midrib* broadly and shallowly sunken to flat-sunken above, 5–20 mm diam., convex and bluntly low-triangular below, drying light brown to dark brown paler than surface below; *pri-*

mary lateral veins 14 to 21 per side, departing midrib at a mostly 30°–40° angle above middle, often 70°–90°, often arising at an acute angle, spreading to the margins, broadly curved toward apex, eventually merging at margins, weakly sunken above, weakly convex below, drying brownish and darker than surface below; the interprimary veins usually darker than surface, 1 between each pair of primary lateral veins; minor veins visible, slightly darker than surface, drying moderately obscure on lower surface. INFLORESCENCES 3 to 6 per axil; *peduncle* 8.5–19 cm long (averaging 13.5 cm), 3–6 mm diam., drying striate; *spathe* 14.5–32.5 cm long, 4–5.5 cm diam. (averaging 20.8 cm long), 2.5–4 cm diam. at constriction, 0.9–2.3 times longer than the peduncle (averaging 1.5 times longer than the peduncle), gradually long-tapered toward apex from midway, light green to medium green throughout; spathe tube 3 × 2.3 cm diam. when furled (flattening 4.0–5.5 cm wide), the constricted area flattening 2.5–4.0 cm wide; spathe blade 2.5–4 cm wide at anthesis; *spadix* 13–27 cm long (averaging 17.4 cm long); free portion 10–13.5 cm long; pistillate portion to (6.5)8–10.8 cm long (averaging 8.3 cm long), 8–17 mm wide, drying 8 mm diam.; fertile staminate portion 8.3–12 cm long, cream-colored, moderately tapered toward apex and weakly tapered toward base, 7–12 mm diam. midway; mostly sterile intermediate segment 1.7–3.7 cm long, with a few scattered staminodia throughout; pistils 43 to 69, irregularly scattered, nearly contiguous, 3 to 4(6 to 7) dispersed across spadix width, separated from one another by up to 4 times their width; ovary depressed-globose, 2 mm long, yellow-green; stigma cushion-shaped, 2.8–3.4 mm diam., about twice as wide as thick and usually broader than the pistil at anthesis, yellowish; staminodia white, 3 to 5 per pistil, 3–4 mm long, free or briefly united at base; synandria 1.6–3.0 mm diam., subrounded, depressed medially at apex, drying orange-brown. INFRUCTESCENCE 19–24 cm long; spathe orange outside; spadix 8–15 cm long; *berries* red, subglobose, ovoid to ellipsoid, 7–10 mm long.

Distribution and habitat. *Dieffenbachia horichii* is known only from the Pacific slope of Costa Rica from the Carara reserve and Puriscal region to the San Isidro region and Dominical. It occurs in *Premontane rain forest* (P-rf) and transition forests between *Tropical wet forest* (T-wf) and *Premontane rain forest* (P-rf) life zones (Holdridge, 1967), from sea level to 900 m.

Phenology. *Dieffenbachia horichii* begins to flower in the early rainy season from May to July, but flowering collections have also been seen in September. Immature inflorescences have been seen from November to May, and mature fruits have been seen from the late rainy season (November) to early rainy season (late June).

Discussion. The species is characterized by its fully sheathed petioles, involute petiolar sheath, and by its thick and more or less elliptic, semiglossy to glossy, mostly unvariegated blades that dry somewhat greenish to yellow-brown.

Dieffenbachia horichii is closely related to two other species with petioles fully sheathed or nearly so. These are *D. panamensis* and *D. standleyi*. In comparison with *D. horichii*, *D. panamensis* has similarly shaped blades and petioles fully sheathed, but that species differs in having the petiole sheath usually flaring and recurled rather than involute as in *D. horichii*. It also has leaf blades with the upper surface matte and subvelvety that dry blackened. Another difference is that *D. panamensis* occurs principally on the Atlantic slope of central Panama, whereas *D. horichii* occurs on the Pacific slope of Costa Rica.

Dieffenbachia horichii is likely to be confused with *D. standleyi*, another species with fully or mostly winged petioles. That species occurs on the Atlantic slope of Honduras and Nicaragua, and differs by having the petiole sheath erect and recurled outward along the margins and acute at the apex with the sheath margins markedly undulate (vs. the sheath margins involute and smooth). The petioles of *D. standleyi* are also longer on average, frequently more than 25 cm long, and average 30 cm long (vs. frequently less than 25 cm long, averaging less than 20 cm long for *D. horichii*). In addition, the upper midrib on the blades of *D. standleyi* is broadly concave, whereas on *D. horichii* the midrib is broadly convex with a medial sulcus but with the entire midrib sunken in a valley.

Most of the typical material of *D. standleyi* has been collected in the Lancetilla Valley and its vicinity in Honduras, and has blades considerably longer on average than those of *D. horichii*. Some collections in Nicaragua and in western Costa Rica are unusual. *Stevens 7457* from Zelaya and *Moreno 17142* from Matagalpa dry a darker yellow-brown. The only other species in Central America that has a fully sheathed petiole is *D. tonduzii*. *Dieffenbachia tonduzii* is distinguished by having smaller and thinner blades (rarely to 45 cm long and 20 cm wide) that are usually matte to weakly glossy above (vs. usually glossy in *D. horichii*) with more primary lateral veins (18 to 25 vs. usually fewer than 20 in *D. horichii*). *Grayum 4757*, from the Carara Reserve in Puntarenas Province, is perhaps a hybrid

between *D. horichii* (*Grayum 4756*) and *D. oerstedii* (*Grayum 4765*). It differs in having petioles that are narrower and less fully sheathed.

Etymology. The species is named in honor of horticulturist Clarence Horich, who made the first collection of the species.

Paratypes. COSTA RICA. **Puntarenas:** San José Province, Playa Dominical-San Isidro del General Baru, Tinamastes, *Burger et al. 10669* (F, MO), *Burger & Baker 10137* (CR, F); along Quebrada Bonita, Carara Res., *Grayum et al. 5723* (INB, MO); Finca El Edén, km 183, R. 2, ca. 400 m E of Santa Marta, *L. Gómez 22951* (B, CM, CR, MO); Quebrada Bonita, Carara Res., *Grayum 4756* (CR, MO), *Croat 79073* (EAP, INB, MO, PMA); hills at SW part of Montañas Jamaica, ca. 2.5 km NE of Bijagual de Turrubares, Carara Res., *Grayum et al. 5467* (MO). **San José:** Par. Nac. Braulio Carrillo, Quebrada Sanguijuela, *Chavarría & Umaña 157* (CR, MO); Zona Prot. La Cangreja, vic. Quebrada Grande, ca. 2 km NNE of Mastatal de Puriscal, *Grayum 8638* (CR, MO); ZP La Cangreja, ca. 1.5 km E of Santa Rosa de Puriscal, *Grayum et al. 8336* (CR, MO); San José rd. from Parrita to Santiago de Purriscal, *Barringer 1790B* (CR); Res. Biol. Carara-Est. Quebrada Bonita, *Chacón 1406* (CR); Cordillera Talamanca, Río Hermoso, Finca El Quizarra, *L. Williams et al. 28479* (F, NY, US); Acosta, along Río Parritilla, ca. 1 km E of Zoncuano, *Grayum et al. 11174* (INB, MO); Pérez Zeledón, Fila Tinamaste, *Valverde 741* (CR, MO); Puriscal, Fila Túfares, Salitrales de Puriscal, *Gómez-Laurito 7792* (CR); Z.P. La Cangreja, Cerros de Puriscal, San Martín de Puriscal, La Fila Vara Blanca, *J. Morales 2035* (CR, INB, MO).

Cultivated specimens. Costa Rica. 800–900 m, cultivated at Munich as 1203/74, *Horich s.n.* (M).

14. Dieffenbachia isthmia Croat, sp. nov. TYPE: Panama: along trail betw. Río Maje & Quebrada Brava, 60 m, 4 May 1976, *T. B. Croat 34656* (holotype, MO-240198!; isotypes, B!, K!, PMA!, US!). Figures 14, 28A.

Planta plerumque ad 1 m; internodia 0.5–3 cm longa, 2–3(4.5) cm diam., atroviridia; petiolus 11–34(40) cm longus, vaginatus 0.4–0.77 longitudinis, vagina 8.5–21 cm longa; lamina oblongo-ovata vel anguste ovata, (12)15–30(39) cm longa, (6)10–26 cm lata, plerumque subcordata, nervis primariis lateralibus 7–12(15) utroque; inflorescentia 3–5 per quoque axillam; pedunculus (2.5)4–12.5 cm longus; spatha 15–17.5(23) cm longa, spadix 10.5–15.8 cm longus; pars feminea 6.5–9.5 cm longa, 1.4 cm diam.; pars masculina 6–7.5 cm longa.

Medium-sized herb, usually to no more than 1 m tall (rarely to 1.5 m tall); sap watery, sometimes white; stem creeping over surface of ground at base, then erect; *internodes* weakly glossy, 0.5–3 cm long, 2–3(4.5) cm diam., dark green, drying dark yellow-brown, olive-brown to blackened. LEAVES scattered along stem, denser near apex; *petioles* 11–34(40) cm long, (averaging 26 cm long), moderately soft, sheathing to midway or slightly above, for 0.4–0.77 their length (averaging 0.55 their length); sheath 8.5–21 cm long (averaging 14 cm), with margins drying thin, light brown and minutely undulate, the tip inequilaterally acute to emarginate and free-ending; unsheathed portion flattened or rounded and becoming weakly sulcate toward apex in cross section (never sharply sulcate), blunt to moderately acute, rarely broadly and bluntly sulcate; *blades* oblong-ovate to narrowly ovate, (12)15–30(39) cm long, (6)10–26 cm wide (averaging 26 × 16 cm), 0.78–1.77 times longer than petiole (averaging 1.1 times longer), inequilateral, one side 0.5–2.6 cm wider than the other side, thinly coriaceous, abruptly to gradually acuminate at apex, acute to cordate at base, the sides often ± unequal, usually subcordate with at least one side subcordate at base; upper surface matte to weakly glossy, dark green, drying dark gray-green to sometimes blackened; lower surface matte, paler, drying yellowish gray-brown to dark yellow-brown; *midrib* 5–8 mm diam., flat to broadly and obscurely sunken at base, weakly raised toward apex above, concolorous to slightly paler than surface, frequently much paler than surface or even white toward apex, often with a light green streak distally, drying paler than surface or darker than surface above, convex to bluntly round-raised, drying somewhat flattened with acute ribs below, drying darker than surface below; *primary lateral veins* 7 to 12(15) per side, departing midrib at a 45°–55° angle (to 30°–50° at apex, 50°–90° at base), arising acutely, then spreading weakly or not at all sunken, often greenish toward apex, sometimes raised near midrib, and diminishing toward margins above; minor veins obscure above, obscurely visible to not visible below. INFLORESCENCES straight to slightly curved, 3 to 5 per axil, bracteoles 9–20 cm long; *peduncle* (2.5)4–12.5 cm long, 6–10 mm diam., sometimes flattened on one side in cross section, green; *spathe* 15–17.5(23) cm long, medium green outside, slightly paler green inside throughout, except the apical portion white at anthesis, to 1.7 cm longer than the spadix, elongating somewhat after closing; spathe tube less than 2 cm diam. when furled, spathe blade 2.5–3 cm diam. at anthesis; *spadix* 10.5–15.8 cm long; free portion 7–13 cm long, 6–8 mm diam.; pistillate portion 6.5–9.5 cm long, to 1.4 cm diam. throughout; fertile staminate portion 6–7.5 cm long, 9–10 mm diam. throughout; sterile intermediate segment 2 cm long, with a few staminodia scattered throughout its length, drying ca. 3 mm wide; pistils 30 to 51, closely spaced except near apex, ovary 3–3.2 mm diam., medium green to dark yellow; stigma 2.4–2.7 mm diam.; staminodia white, 2.5–3.5 mm long, flattened near base, subglobular at apex; synandria 2.6–3.2 mm diam., drying irregu-

Figure 14. *Dieffenbachia isthmia* (*Croat & Zhu 77115*). —A. Leaf blade adaxial surface. —B. Close-up of petioles showing inflorescence. —C. Close-up of female portion of spadix showing pistils and staminodes. —D. Infructescences, one cut off to show the fruits.

larly somewhat rounded, margins often irregularly turned upward. INFRUCTESCENCE with spathe to 23.5 cm long, usually orange; spadix, 9–12 cm long, ca. 3 cm wide; *berries* orange to red or orange-red, drying pale yellow-brown, ellipsoid, 7–8 mm long, 6 mm diam. (the stigmatic area ca. 2 mm wide); seeds drying dark brown, 6 mm long, 5 mm diam., to 3 mm thick, moderately smooth, caved outward on funicular side.

Distribution and habitat. *Dieffenbachia isthmia* ranges from Panama to Colombia (Antioquia and Chocó). The species is highly variable ecologically, occurring principally in *Tropical moist forest* (T-mf) and drier parts of *Premontane wet forest* (P-wf) life zones at 50–800(1000) m elevation, but also in *Premontane moist forest* (P-mf), *Premontane wet forest* (P-wf), and *Tropical wet forest* (T-wf) life zones (Holdridge, 1967) in Colombia. In Panama, the species ranges from Veraguas Province to the Azuero Peninsula in the west (700–900 m in Herrera and Los Santos Provinces).

Phenology. Flowering for *D. isthmia* occurs in the early rainy season from May to September (rarely in November), with fruits maturing during the dry season and early rainy season of the following year, mostly in April and May, but with many collections made in fruit from August to October.

Discussion. The species is characterized by its moderately small (usually less than 1 m tall and with stems usually less less than 2.5 cm diam.) habit and frequently subcordate blackish-drying blades which often have a white streak on the distil half of the flattened (not flat-raised) midrib. In Panama, it is probably most easily confused with *D. killipii*, which differs in having proportionately narrower (typically only to 16 cm), usually subcordate greenish-drying blades with the upper midrib weakly flat-raised rather than merely flattened above.

Though its range does not overlap with *D. isthmia*, *D. oerstedii* may be confused with this species. The latter, ranging from Mexico to central Panama, differs in having a usually sharply sulcate petiole and blades that dry greenish to yellowish green rather than blackened as is usually the case in *D. isthmia*.

Etymology. The species epithet "isthmia" refers to its dominance in the area of the Isthmus of Panama.

Paratypes. PANAMA. **Canal Area:** Barro Colorado Island, *Aviles 24* (MO), *Shattuck 397* (MO); Lutz Trail, *Croat 5378* (F, MO, RSA, SCZ, STRI), *Croat 10133* (MO), *Croat 5317* (MO), *Croat 5896* (MO), *Croat 7712* (MO), *Croat 11291* (F, NY, SCZ), *Croat 5183* (MO), *Croat 10982* (MO, SCZ), *Croat 5709* (MO), *Foster 865* (DUKE), *Luteyn & Croat 906* (DUKE), *Croat 15173* (MO), *Croat 5819* (MO), *Croat 6308* (MO), *Croat 6502* (MO, PMA), *Croat 4576* (MO), *Killip 39979* (US), *Kenoyer 188* (US); 12 mi. S of Colón on Río Providencia, *Tyson & Blum 3998* (PMA); Frijoles vic., *Pittier 3754* (US), *Bailey 335* (F); Gatun Lake, *Standley 41107* (US), *Standley 40960* (US), *Maxon et al. 6812* (US), *Maxon et al. 6820* (US), *Standley 31266* (US); Río Paraiso, above East Paraiso, *Standley 29867* (US). **Colón:** Río Guanche, ca. 5 km upstream from rd. to Portobelo, *Hammel & Trainer 14767* (MO). **Darién:** PN Cerro Pirre, vic. Río Perisenico, *Croat & Zhu 77115* (INB, MO); 112 mi. E of Bayano Dam Bridge, vic. Canglón, *Antonio 4546* (MO, PMA); trail from Cana to Colombian border along Río Setgandí, *Gentry et al. 28574* (COL, MO); El Real-Pinogana, *Duke 5014* (MO); 3 mi. N of Santa Fe, *Tyson et al. 4631* (SCZ), *4632* (MO, SCZ); 2 mi. E of Santa Fe, *Tyson et al. 4834* (STRI); PN del Darién, between Río Topalisa & Río Pucuro, ca. 17 km E of Pucuro, La Laguna area, *Hammel et al. 16262* (CAS, COL, MO, PMA); airstrip at Cana gold mine area, *Croat 38010* (MO), *38057* (MO); S of El Real, Alturas de Nique, near Cana mine, rd. to Boca de Cupe, *McPherson 11591* (MO); Cana region, ca. 1.5 km from Cana trail to Boca de Cupe, *McPherson 15037* (MO). **Herrera:** W of Las Minas, near Chepo, on Montosa de Chepo, *McPherson 10958* (MO); Dist. Las Minas, Chepo, loma El Montuoso, *Galdames et al. 1626* (MO, PMA, US); Las Minas, base of El Higo, *Galdames et al. 2486* (PMA, US). **Los Santos:** Loma Prieta, Cerro Grande, *Lewis et al. 2195* (COL, DUKE, MO, UC). **Panamá:** Distrito Chepo, Puerto Coquira, *Zambrano & Delgado 1336* (PMA); San José Island, *I. Johnston 1165* (GH); vic. Bayano Lake dam near Canita, *Gentry & Tyson 1653* (MO, PMA); Chimán, *Lewis et al. 3251* (MO); 3.8 mi. E of Río Ipetí, lower slopes of Serranía de Majé, *Hufi & Jacobs 1997* (MO); Río Majo-Quebrada Brava, ca. 2 mi. upstream from waterfalls near edge of Bayano Lake, *Croat 34745* (MO); Isla Bayano, *Garibaldi 68* (MO); near Chiman, ca. 2 mi. up Río La Maestra, *Kennedy 1193* (F). **Veraguas:** near proposed route of rd. from El Cortezo to Arenas, *Hammel 5378* (MO); Azuero Peninsula, trail between Jobero and headwaters of Río Pedregal, *Croat 34475* (COL, F, MO, PMA); 18 km W of Las Minas, Cerro Alto Higo, *Hammel 4298* (MO); "Los Girasoles," Escuela Agrícola Alto Piedra, ca. 5 km NW of Santa Fé, *Dressler 4716* (DUKE, F, MO, PMA); 18 km W of Las Minas, Cerro Alto Higo, *Hammel 4298* (MO); Cerro Delgadito just NW of Cerro Tuté, S of Santa Fe, *Luteyn 4043* (DUKE); Dist. Montijo, Isla Coiba, Cerro de La Torre, *Galdames et al. 2286* (MO); Isla Coiba, Río Escondido vic., *Galdames et al. 2252* (MO). COLOMBIA. **Antioquia:** Mutatá, Bajira-Nuevo Oriente Road, *Brand & Ascanio 277* (COL). **Chocó:** Ríosucio, PN Natural Los Catios, Campamento de Tilupo, *Forero et al. 1723* (COL, MO).

15. Dieffenbachia killipii Croat, sp. nov. TYPE: Panama. Coclé: vic. of El Valle de Antón, La Mesa, forested flat area near Finca Macarenita, 8°36′N, 80°07′W, 800 m, 6 July 1994, *T. B. Croat & G. Zhu 76666* (holotype, MO-04612287!; isotypes, AAU!, B!, CAS!, COL!, CR!, DUKE!, F!, GH!, HUA!, INB!, K!, M!, MEXU!, NY!, PMA!, SCZ!, US!, VEN!, WU!). Figure 15, 28B.

Planta terrestris, 40–100 cm.; internodia 1.5–5.5 cm

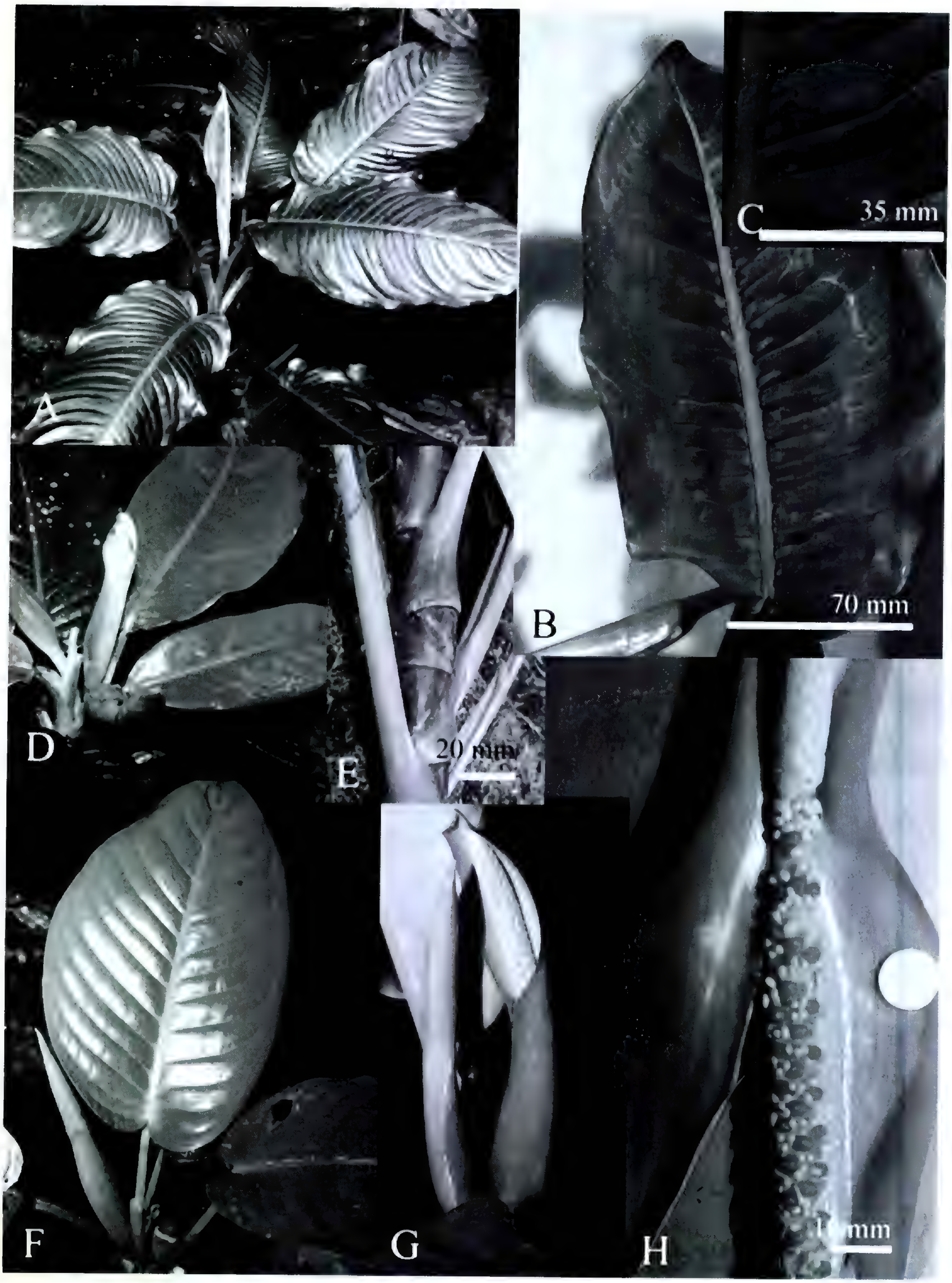


Figure 15. *Dieffenbachia killipii*. —A. Habit showing plant with quilted primary lateral veins (*Croat 56902*). —B. Leaf blade adaxial surface (*Croat 78247*). —C. Close-up of adaxial surface of blade (*Croat 74759*). —D. Habit of flowering plant (*Croat 76666*). E, G. (*Croat 75154*). —E. Close-up of stems. —F. Habit of flowering plant (*Croat 76666*). —G. Close-up of two inflorescences, one at anthesis. —H. Close-up of pistillate and sterile staminate portions of spadix (*Croat 76259*).

longa, (0.8)1.5–3(4) cm diam; petiolus (4)6–20(24.5) cm longus, vaginatus 2/5 longitudinis vel fere omnino; lamina oblongo-elliptica vel oblongo-ovato, (13)19–30(33.5) cm longa, (4.5)7–16(21.3) cm lata, nervis primariis lateralibus 8–12 utroque; inflorescentia 1–4 in quoque axilla; pedunculus 4.5–9 cm longus; spatha 12–19 cm longa; spadix 12–15 cm longus; pistilla 20–37.

Medium-sized herb, 40–100 cm tall, stem creeping over surface of ground at base, then erect; sap milky, unscented; *internodes* initially weakly glossy, often faintly dark green and medium yellowish green-marbled at lower nodes, becoming glossier in age, 1.5–5.5 cm long, (0.8)1.5–3(4) cm diam., medium to dark green or olive-green or black-green, drying dark yellow-brown to orange-brown, rarely dark brown, epidermis sometimes fissured in a cracked network so as to appear corky in some areas. LEAVES scattered along stem, denser near apex; *petioles* (4)6–20(24.5) cm long (averaging 12.2 cm long), firm to spongy, slightly paler or darker than stem, medium green to dark green, matte to weakly glossy, faintly striate toward the base, drying greenish to grayish yellow to brown, sheathing for ⅖ to fully throughout (0.4–1 the petiole length and averaging 0.69); sheath 3–18 cm long, (averaging 8 cm), with the sheath margins not drying markedly different than the remainder of sheath; sheath apex with the tip free-ending and inequilaterally acute to emarginate, sometimes drying acute; unsheathed portion C-shaped and sharply sulcate to narrowly and sharply sulcate to subterete and weakly sulcate or obtusely and narrowly sulcate in cross section; *blades* oblong-elliptic to oblong-ovate, rarely narrowly ovate, (13)19–30(33.5) × (4.5)7–16(21.3) cm (averaging 25 × 11 cm), 1.5–4.2 times longer than wide, as long as or up to 4.8 times longer than petiole (averaging 2.3 times longer than petiole), inequilateral, one side 0.5–1.5 cm wider than the other side, sometimes falcate, subcoriaceous to weakly coriaceous, moderately bicolorous, acuminate to gradually acuminate at apex inequilateral, sometimes inequilaterally rounded to subcordate, rarely acute at base; margins moderately straight on one side, frequently markedly undulate on other side; upper surface semiglossy, dark green, frequently white, pale green or yellowish green-spotted or white-streaked, drying dark brown to olive-brown or gray-green; lower surface paler, matte to weakly glossy, drying yellow-brown; sinus less than 1 cm deep, rarely to 2.5 cm deep; *midrib* flat-raised, 3–5 mm wide, sometimes sulcate toward base, usually in moderately deep valleys, usually concolorous, sometimes paler than surface above, sometimes weakly 3- to 4-grooved on upper surface, drying flat-raised to broadly convex, slightly paler to concolorous above, thicker than broad and narrowly rounded to almost round-raised, matte, paler than surface to almost concolorous below, drying brown with ridges, darker than surface below; *primary lateral veins* 8 to 12 per side, arising at an acute angle, then spreading at mostly (40°)45°–70° angle (rarely to 30°, sometimes to 80° toward base, rarely to 110° at base), frequently forming collective veins that merge with the margin higher up on the blade, narrowly sunken to weakly quilted-sunken above, thicker than broad to convex and weakly pleated-raised, darker than surface to almost concolorous below, usually drying darker than surface; minor veins few, obscure above, obscurely visible and darker than surface to moderately distinct below. INFLORESCENCES 1 to 4 per axil; bracts 9–20 cm long; *peduncle* 4.5–9 cm long, 6–7 mm diam., medium green, white at base; *spathe* 12–19 cm long at anthesis, 1–2 cm longer than the spadix, medium green throughout, sometimes faintly dark green-lineate on faded areas outside, slightly paler and glossy inside; spathe tube 2–3 cm diam. when closed, 5.5–7.5 cm wide when flattened, 1.5–2 cm diam. at constriction (flattening 3.5–4 cm wide); spathe blade 2.5–3 cm diam.; *spadix* bluntly pointed, weakly protruding forward at anthesis, 12–15 cm long; free portion 5.5–6 cm long (sometimes with a few pistillate flowers in the basal portion); pistillate portion 5–8.5 cm long, 10 mm diam. throughout; fertile staminate portion 4.5–6.8 cm long, 7–8 mm diam. midway, sometimes bluntly pointed (frequently with the withered portion weakly protruding out of the front of the spathe after anthesis); sterile intermediate segment to ca. 5 mm diam., but usually absent with the pistillate and staminate portions almost contiguous; pistils 20 to 37, well-spaced, sometimes aggregated into weak rows, frequently irregularly gapped, 2 or 3(6) dispersed across spadix width, widely spaced at base and at apex, pale yellow-green, 2.4 mm diam., 1.4 mm high; stigma 1.8–2.2 mm diam.; staminodia very thickened and mostly joined at base, tapered gradually toward apex and not markedly thickened, sometimes broadened laterally and apparently consisting of a union of 2 staminodia, sometimes with 2 pistils contiguous and apparently sharing staminodia; synandria 1.2–1.4 mm diam., ca. 4 per spiral, irregularly rounded to 4- to 6-sided, drying widely spaced, the margins of apex markedly turned upward. INFRUCTESCENCE to 23 cm long; spathe orange outside; *spadix* 9–10.5 cm long, 2.5 cm wide; *berries* red to reddish orange or orange-red, drying pale orange-brown, ellipsoid, 2- to 3-lobed, 7–8 mm long, 6–10 mm diam.; seeds 1 to 2 per berry, drying dark

brown, flattened on funicular side, to 4.9 mm long, 4.4 mm diam., drying smooth, 3 mm thick.

Distribution and habitat. *Dieffenbachia killipii* ranges from southwestern Costa Rica (Puntarenas) to Panama and the western slopes of the Andes in Colombia (Antioquia, Chocó, Tolima, and Valle) and Ecuador (Esmeraldas, Guayas, El Oro, Pichincha, Los Ríos, and Manabí on the Pacific slope and in Napo on the Atlantic slope) at 0 to 900 m elevation. In Panama it occurs in *Tropical wet forest* (T-wf) and *Premontane wet forest* (P-wf) life zones (Holdridge, 1967) and ranges from Coclé Province to Darién Province in the east. In Colombia it is known from *Tropical wet forest* (T-wf) and *Tropical rain forest* transition to *Premontane wet forest* (T-rf/P-wf) life zones.

Phenology. Flowering occurs in *D. killipii* throughout the year, with most flowering specimens having been made in the late rainy season from September to November. Fruiting collections were made mostly during the late dry season and early rainy season of the following year from May to July. Few fruiting collections were seen between August and May.

Discussion. The species is characterized by its medium stature (to 1 m), slender sulcate petioles with the sheath inequilaterally auriculate at apex (and usually ending well below the base of the blade), and especially by the frequently subcordate blades (which dry yellowish green) with a flat-raised midrib. Also unusual for the species is the near absence of a sterile portion between the pistillate and staminate spadices.

Dieffenbachia killipii is similar to *D. leopoldii*, which was described from a cultivated plant of unknown specific origin, believed to have been obtained in Colombia. Engler saw living material of this species and illustrated it in his 1915 revision. While it has very similar leaves, *D. leopoldii* differs from *D. killipii* in having the pistillate and staminate portion of the spadix separated by a sparsely flowered, almost sterile section. In addition, while the upper surface of *D. killipii* is semiglossy, *D. leopoldii* is described as having a blade "velvety green" on the upper surface in the notes of N. E. Brown (on specimen of *Lehmann 1052*), at least suggesting that the upper surface was matte. Finally, the midrib of *D. leopoldii* is described as white, whereas this is not the case with *D. killipii*.

Collections from the eastern slopes of the Andes in Napo Province, Ecuador, appear also to be this species but more studies are needed to confirm this, as they would be the only collections of *D. killipii* in the Amazon basin. The collections include *Croat 50480* and *Plowman & Davis 4094*, both collected along the Baeza to Tena Road, at 1410 and ca. 1743 m, respectively, and *Croat 72573* south of Coca at 300 m. An unvouchered collection made by Tan, Halton, and Besse at the Auca Oil Field at 240 m is also the same species. It has been vouchered from the Marie Selby Botanical Gardens' living collection (SEL 79-0090) by *Plowman 14121* and *Ingram 1124*.

Gentry et al. 65306, from Quindío Department, Colombia, at 1400 m, may also be this species, but it is from higher elevation than other Colombian collections. A collection made in Venezuela at Maiquetía at 30 m near the Caribbean (*André 457A*) appears to also be *D. killipii*. However, this may be questioned because *Andre 457* was labeled as having been collected in Colombia at Angostura de Honda (Tolima). Both collections were dated December 1875.

In South America the species may be confused with *D. enderi*, described from the valley of the Río Cauca in Colombia. That species is similar in having the petiole sheath auriculate and free-ending at the apex, and in having the staminate and pistillate spadices contiguous. It differs in having a thicker stem (to 8–9 cm diam.), longer blades (to 50 cm long) with acute bases and more numerous primary lateral veins (ca. 24 per side, spaced 1.5–2 cm apart). In contrast, *D. killipii* has blades that are rounded or subcordate at the base, and fewer than 15 primary lateral veins. It is also similar to *D. daguensis* from the valley of the Río Dagua in Valle Department, which similarly has staminate and pistillate zones contiguous on the spadix. That species differs in having larger blades (to 40 cm long) with many close primary lateral veins (up to 25), and a petiole only 5 cm long.

Dieffenbachia killipii is probably most easily confused in Central America with *D. isthmia*, which differs in having stems that dry usually blackened; somewhat more ovate, blackened blades; and a spadix with a more or less sterile portion between the staminate and pistillate portions. The species may also be confused with *D. oerstedii* from Costa Rica and western Panama. That species shares leaves of similar shape and size, but it has blades that are matte, rather than semiglossy, on the upper surface and dry greenish or yellowish green. In addition, *D. oerstedii* has petioles that are typically more sharply sulcate than those of *D. killipii*. The petiole base is green in *D. killipii* and whitish in *D. oerstedii*. Furthermore, the spadix has staminate and pistillate portions nearly contiguous in *D. killipii*, but separated by a distinct sterile portion in *D. oerstedii*.

In Panama the ranges of *D. oerstedii* and *D. killipii* do not actually overlap, but come close in Chiriquí on the western slopes of the country. All known collections there occur in the mountains at 900 to 1300 m. *Dieffenbachia oerstedii* occurs in Panama in western Chiriquí Province at highland sites and with an outlying population at El Copé in Coclé Province, while *D. killipii* ranges in general no further west than the Azuero Peninsula and Veraguas Province in Panama. There is an unusual outlying population of *D. killipii* in the area of the Osa Peninsula in Costa Rica (*Kennedy 1594*). A collection from Cerro Colorado (*Croat 48437*) in Chiriquí Province has blades slightly larger than most specimens of the species.

Croat 74789 from La Mesa in Coclé Province, Panama, is unusual in having a series of rather prominent collective veins and in having the minor veins distinct when fresh (typically they are rather obscure). It was, in fact, so unusual that it was initially mistaken for a *Xanthosoma*. It is, however, within the degree of variation for *D. killipii*.

Kress 77-830 and *77-831* from the vicinity of Santa Fe in Veraguas, Panama, are unusual collections in having the staminate and pistillate portions of the spadix separated by as much as 1 cm. In this regard they are similar to *D. lutheri*, but differ from that species in lacking the granular puberulent major veins on the lower blade surface.

Some collections of the species from Darién Province, Panama (e.g., *Antonio & Hahn 4405*, *Duke 15591*, *Polanco 1485*, and *Schmalzel 1212*), are unusual in having petioles more fully sheathed, sometimes to less than 1 cm from the base of the blade or even with the petiole sheathed throughout.

The Costa Rican population of *D. killipii* is noteworthy in that the single collection made there in the Osa Peninsula is quite disjunct from the nearest population in Panama, where the species has not been collected west of Coclé Province. The species is to be expected at other sites in Veraguas and in Chiriquí Province, Panama.

Etymology. The species is named in honor of the late E. P. Killip, botanist at the U.S. National Herbarium and one of the more prodigious plant collectors in the Neotropics, who was one of the earliest collectors of this new species.

Paratypes. COSTA RICA. **Puntarenas:** Osa Peninsula, 2.5 mi. SW of Rincón, *Kennedy 1594* (MO). PANAMA. **Bocas del Toro:** Cerro de Bocatorito, *Peterson & Annable 6768* (MO). **Canal Area:** 12 mi. S of Colón, *Tyson et al. 4486* (SCZ); 12 mi. S of Colón, near Río Providencia, *Tyson & Blum 3997* (MO, SCZ); Pipeline Rd. 10 mi. from Gamboa gate, *Croat 15082* (DUKE, MO); ca. 7–8 km N of Gamboa, *Knapp 2275* (MO); Pipeline Rd. near Gamboa, *Clewell & Tyson 3306* (MO, SCZ); Pipeline Rd. at Río Agua Salud, *Croat 12353* (MO); Río Frijol on Pipeline Rd., 6 m N of Gamboa, *Tyson 1443* (FSU, MO, SCZ); Frijoles-Monte Lirio, *Killip 12154* (US); N of Frijoles, *Standley 27413* (US); W of the Canal, near Gatún, *Standley 27224* US); rd. S-10 N of Escobal near junction with Rd. S-1, *Croat 12489* (MO); 1.5 mi. N of Escobal, *Croat 12491* (MO, SCZ); near Limbo Gun Club camp, 10 mi. W of Gamboa on Pipeline Rd., *Lazor & Tyson 3492* (FSU); lake shore along Gatun River valley, *Pittier 6845* (US); vic. Gamboa, *Pittier 2600* (US); Pipeline Rd. N of Gamboa, *Kennedy 455* (F). **Chiriquí:** 8.8 km past Gualaca on rd. to Chiriquí Grande, *Hoover 1324* (MO); Gualaca-Fortuna Dam site, 2.8 mi. beyond Los Planes, *Croat 48816* (MO); Cerro Colorado, 15.6 mi. above Río San Felix, *Croat 48437* (MO). **Coclé:** El Limón, *Mendieta 1-10* (PMA), *Mendieta 1-101* (PMA), *Mendieta 1-121* (PMA); vic. of El Copé, PN El Copé, 5–6 mi. N of El Copé, below Old Rivera saw works area, *Croat & Zhu 76746* (CAS, DUKE, MO); 5 hours' walk N from Alto Calvario to Río Blanco, *Sytsma et al. 2414* (MO); La Mesa, above El Valle de Antón, *Croat 14388* (MO), *Croat 14309* (MO); trail beyond La Mesa towards Los Llanos and the border between Coclé and Panamá Provinces, N of El Valle de Antón, *Luteyn 3175* (DUKE), *Croat 37383* (MO); La Mesa above El Valle, *Gentry 7423* (MO, NY); 5 mi. N of El Valle de Antón, *Luteyn 1203* (DUKE); La Mesa trail towards Cerro Caracoral, NE of El Valle de Antón, *Luteyn 3180* (DUKE); vic. El Valle, *Bartlett & Lasser 16678* (MEXU, MO); Penonomé-Coclecito, 5.6 mi. N of Llano Grande, along Río Cascajál 5.6 mi. N of Llano Grande, 1.4 mi. N of Cont. Divide, *Croat 67480* (MO, SCZ); at La Mesa, 3.2 mi. above El Valle, 0.1 km E of Finca Macarenita, *Croat 74789* (MO), *Croat 74792* (INB, MO, PMA); ca. 1 km W of rd. betw. Finca Mandarinas and Finca Furlong, *Croat 67197* (MO); area between Caño Blanco del Norte, Caño Sucio and Chorro del Río Tife, *Davidse & Hamilton 23599* (MO); rd. to Coclesito, logging camp 12 mi. from Llano Grande, *Churchill et al. 4032* (MO), *Churchill et al. 4125* (MO); 7 km N of El Copé, near Rivera Sawmill, *Folsom & Collins 6436* (MO); La Mesa, above El Valle de Antón, ca. 2 km W of Cerro Pilón, *Croat 37479* (MO, PMA, WU); base of Cerro Pilón above El Valle, *Gentry & Dwyer 3643* (DUKE, F, MO). **Colón:** PN Chagres, Sección Boquerón, Río San Juan de Pequení, *Espinosa et al. 3611* (PMA), *Espinosa & Guerra 3762* (PMA), *Espinosa et al. 4478* (PMA); Dist. Donoso, Campamento Botija, *J. Polanco et al. 1905* (PMA); Río Providencia, 12 mi. S of Colón, *Tyson & Blum 3954* (FSU, SCZ); Río Guanche, between Puerto Pilón and Portobelo, ca. 1.5 mi. S of rd., *Croat & Zhu 76253* (MO, PMA), *Croat & Zhu 76259* (MO, SEL, SCZ); lower Río Guanche, *Dressler 4688* (PMA); N of Río Guanche, *Davidse & D'Arcy 10098* (MO); Río Guanche, 3–5 km above bridge on Colón-Portobelo Rd., *Croat 79329* (MO), *Croat 79359* (MO), *Sytsma 1658* (MO); near Peluca, km 25.6 from Transisthmian Hwy. on rd. to Nombre de Dios, *Kennedy 2661* (MO); ca. 8 km E of Piña, *Thompson 4816* (CM, MO); Portobelo-Nombre de Dios, 1.2 mi. beyond the jct. of rd. to Isla Grande, *Croat 49805* (INB, MO); Nuevo Tonosi-Río Indio, Portobelo-Nombre de Dios, *Croat 33551* (AAU, MO, QCNE); Achiote, *McPherson 9176* (MO); Santa Rita ridge rd., ca. 22 km from transisthmian hwy., *Hammel et al. 14472* (MO). **Darién:** Quebrada Biboto (Peccary) off Río Areti, *Duke 13601* (MO); 1–3 mi. N of Paya, *Duke & Kirkbride 14019* (MO); Río Cocalito, *Whitefoord & Eddy 136* (BM, MEXU, MO); PN Cerro Pirre, vic. headquarters on Río Perisenico, *Croat & Zhu 77102* (COL, HUA, INB, L, MO, NY, QCA, SCZ, TEFH, US, VEN);

Paya-Pucro, *Stern et al. 433* (GH, MO, US); Punta Guayabo Grando to Río Jagué, *Antonio & Hahn 4405* (MO); 5 mi. W of Yaviza, *Schmalzel 1212* (MO), *Schmalzel & Alverson 1199* (MO, PMA); vic. of gold mine at Cana, *Croat 37605* (HUA, INB, K, MO); S of El Real, headwaters of Río Pirre at fork known as Dos Bocas, *Kennedy & Foster 395* (DUKE); Pinogana-Yaviza, *Duke 5169* (MO); 10 mi. S of El Real on Río Pirre, *Duke 5437* (MO); trail from Río Pucro to Quebrada Maskia, *Duke 13082* (MO); Río Tucutí upstream ca. 2 hrs. (piragua) vic. Tucutí, *Duke 5260* (MO); Punta Guayabo Grando-Río Jaqué, *Antonio & Hahn 4406* (MO); Cerro Campamento, S of Cerro Pirre, *Duke 15591* (US); Rancho Frio, halfway up slope of Cerro Pirre from Piji Vasal, *Folsom 6247* (MO); gold mine at Cana, *Sullivan 745* (MO); Bajo Lepe, 7 km al SE of Boca de Cupe, *Polanco 1485* (PMA); base camp Cerro Pirre NP, *Croat 68961* (COL, MO, PMA); PN del Darién, RENARE station, *McDonagh et al. 433* (BM), *439* (BM, MO); Est. Biol. Rancho Frío at N base of Cerro Pirre, ca. 9 km S of El Real, Quebrada Perisenico, *de Nevers et al. 8267* (CAS, MO); Río Coasi, Cana-Coasi trail, *R. Hartman 12488* (K, MO, PMA); Río Pavarando, 10 km NE of Jaqué, *D'Arcy & Sytsma 14498* (MO); Río Pirre, 2.5 mi. above El Real, *Duke 5099* (MO); Río Torti, 38.6 mi. E of Bayano Dam Bridge, near Torti, *Antonio 4638* (MO); Río Tuquesa, *Clezio 221* (MO), *226* (MO); Río Chico, from Yaviza at junction with Río Chucunaque to ca. 1 hr. by outboard from jct., *Burch et al. 1123* (DAV, MO, NY); ca. 10 km upstream from Nazareth, *Hahn 142* (F, MO); Río Jaqué Valley, *Knapp & Mallet 3089* (MO); Río Balsas, *Kursar & Coley 4* (SCZ), *15* (SCZ). **Panamá:** Piria–Cañasas trail near Piria, *Duke 14346* (MO); El Valle de Madroño-La Saena, 2.5 mi. N of El Valle de Madroño, 3.5 mi. N of turnoff to San José, 11.6 mi. N of Las Margaritas, vic. Chepo, valley of Río Mamoní, *Croat & Zhu 77048* (CAS, LPB, MEXU, MO, PMA, NY, SEL, TEX, US); N of Canita, *Croat 14504* (MO); Cerro Campana, 45 km SW of Panama City on Inter-am. Hwy., *Mori & Bolten 7698* (MO); ca. 10 km SW of Capira, *Mori & Kallunki 3591* (MO), *Croat 14706* (MO); above Su Lin Motel, *Porter et al. 4282* (MO); 6.1 mi. above Pan-Am. Hwy., 3.2 mi. beyond park entrance & Guarda Bosque Station, *Croat 74759* (MEXU, MO, PMA, SCZ), *Witherspoon & Witherspoon 8401* (MO), *Carrasquilla & Rincón 304* (MO), *Miller et al. 753* (B, MO, PMA); PN Altos de Campana, Buena Vista, Bejuco, Chame, *Espinosa et al. 3138* (PMA); natural bridge along Madden Lake, *Croat 12401* (DUKE, MO), *Thompson 4593* (CM); Cerro Azul, *Dwyer 2077* (MO), *Croat 17311* (MO); 1 mi. N of Cerro Azul, *Tyson & Blum 4099* (SCZ); 1–2 mi. beyond Goofy Lake, *Gentry et al. 3406* (NY), *Dwyer 4565* (MO), *Sullivan 59* (MO, PMA); rd. past Altos de Pacora, 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above Pan Am. Hwy., *Croat 68679* (MO); El Llano–Cartí rd, 6.9 km N of Pan-am. Hwy., *Folsom 1444* (MO); 4–5 hrs. walk upriver from Torti Arriba, *Folsom et al. 6852* (MO), *Folsom et al. 6848* (MO); near Bayano Dam, *D'Arcy 9420* (MO); Serranía de Majé Trail, Charco Rico-headwater of the Río Ipetí Grande, *Churchill & de Nevers 4333* (MO); Piria-Canasas trail near Piria, *Duke 14346* (US); Cerro Jefe Region, vic. Finca Vega, 2.3 mi. above Lago Cerro Azul, 4.1 mi. above old Pan-Am. Hwy., *Croat 75154* (MO), *Croat 11570* (F, MO, SCZ); Río Maje, above first waterfall, *Croat 34442* (F, MO, PMA); Río Torti, S of Pan-am. Hwy. near village of Upper Torti, *Folsom & Mauseth 7844* (MO). **San Blas:** SW of Puerto Obaldía, *Croat 16803* (MO); Ailigandí, *Hammel & D'Arcy 5018* (MO), *A. Jones & Tejada 275* (PMA); Kuna Yala Nusigandí FS, NW of El Llano–Cartí Rd., *Schatz 1079* (B, K, MO, US). **Veraguas:** rd. beyond Escuela Agrícola Alto Piedra, NW of Santa Fé, Pac. slope, 0.6 mi. beyond fork in rd., *Croat 19056* (MO); Escuela Agricultura above Santa Fe, *Kress 77-830* (DUKE), *77-831* (DUKE). COLOMBIA. **Antioquia:** Río Anorí valley, Quebrada La Tirana-Providencia, 28 km SW of Zaragoza, *Alverson et al. 376* (WIS). **Chocó:** Quibdó-Istmina, 6.6 km S of Quibdó, *Croat & Cogollo 52174* (COL, MO); ca. 10–15 km S of Quibdó, and 8–10 km E, *Grayum et al. 7657* (MO); Sautatá, PN de Los Katios, *Rentería 10680* (HUA); Río Atrato, Tagachi, *Forero et al. 9007* (COL); Bahía Solano, Corr. El Valle, Quebrada Tundó, tributary of Río Valle, *Espina et al. 2902* (MO); San José del Palmar, Río Torito, Finca "Los Guaduales," *Forero et al. 6272* (COL), *6489* (COL). **Tolima:** Angostura de Hondo (Magdalena), *Lehmann s.n.* (K). **Valle:** Bajo Calima Region, Buenaventura-Málaga, km 11, *Croat 69343* (CUVC, MO); Pulpapel Headquarters, *Bay 278* (MO); 5 km N of main Cali-Buenaventura Hwy., *Croat & Bay 75707* (MO); Cali, Vereda Pico de Aguila, *Gamboa et al. 71* (MO); Río Dagua, Buenaventura, *Lehmann 5311* (K). ECUADOR. **Cotopaxi:** Guayacan-Montenegro, N of Pucayacu, *Croat 73792* (QCNE). **Guayas:** Cordillera Chongón-Colonche, Cerro La Torre, *Cornejo & Bonifaz 3107* (GUAY). **El Oro:** ca. 11 km W of Piñas on rd. to Arenillas, *Thompson 160* (MO); 7.6 km from Tahuin on rd. to Piedras, *Thompson 128* (MO); Machala-Loja, 25 km SE of junction in rd. to Piñas, *Croat 50725* (MO, QCNE). **Esmeraldas:** Cerro Mutiles, *Cornejo & Bonifaz 5191* (GUAY); Santo Domingo de los Colorados-Esmeraldas, 90 km NW of Santo Domingo, 8.8 km NW of Quininde, *Croat 55549* (MO); 6 km beyond bridge over Río Esmeraldas (near San Mateo, rd. to Esmeraldas airport), ca. 6.6 km beyond Univ. Techn. Luis Vargas Torres-Est. Exp. Mutile, Río Mutile, *Croat 55629* (HUA, MO, QCA, US); Ibarra-San Lorenzo rd., *Madison et al. 5008* (F, SEL); Hacienda Guayas, ca. 20 km S of Esmeraldas, *Sparre 15499* (S); Río Verde, Businga, *Juncosa 797* (MO, QCA); Res. Forestal de Jardin Tropical, Univ. Tecnica Luis Vargas Torres, *Gentry & Lajones 73108* (GUAY, MO); Bilsa, Quinindé-Bilsa, 6.4 km W of Sto. Domingo-Esmeraldas Hwy., departing ca. 15 km N of Quinindé, *Croat et al. 83804* (DUKE, F, MO); Río Lita, Lita, *Croat 38947* (F, MO, QCA); Eloy Alfaro, Res. Ecol. Cotacachi-Cayapas, Río Bravo Grande, ½ km from Centro Chachi de Corriente Grande, *A. Alvarez & P. Herrera 699* (MO, QCNE); Charco Vicente, Río San Miguel, tributary of Río Cayapas, *Palacios & Tirado 11327* (MO, QCNE); Esmeraldas-Quininde rd., 40–50 km SE of Esmeraldas, *Harling & Andersson 16727* (GB); Esmeraldas-Borbón, 2.5 km W of Borbón, *Croat 71119* (QCNE). **Guayas:** Naranjal-Machala, 13 km S of Naranjal, *Harling & Andersson 19371* (GB); Cañar-Chimborazo, vic. Bucay, *Camp E-3653* (MO, NY, SEL); Cord. Chongón-Colonche, Bosque Protector Loma Alta, *Cornejo & Bonifaz 1195* (GUAY, MO); Loma Alta, *Cornejo & Bonifaz 5210* (GUAY, MO); Capeira, km 12 Guayaquil to Daule, *Dodson & Dodson 11130* (MO, SEL); La Libertad, *Camp E-3599* (MO, NY). **Los Ríos:** El Centinela, Montañas de Ila, Patricia Pilar-24 de Mayo, *Dodson et al. 8415* (MO); Río Blanco, Santo Domingo-Esmeraldas hwy., 3 km S of km 24, *Croat 50684* (MO); Santo Domingo de Los Colorados, Rancho Brahman, ca. 10 km NW of Santo Domingo, *Sparre 14122* (S); Hacienda Zaracay, *Sparre 15182* (S), *Acosta Solís 10896* (F, S); Tsachila Chiguilpe, *Cerón et al. 29159* (QAP); Santo Domingo-Quevedo, km 11.5, Est. Gustavo Orcés, *Quishpe & Dávila 82* (QAP, QCNE); km 41, *Zak et al. 5726* (QCA); vic. of Montalvo, 40 km E of Babahoyo,

Holm-Nielsen et al. 2769 (AAU, NY, QCNE, S); Hacienda Monica, 12 km E of San Carlos, *Sparre 19397* (S); Hacienda Clementina, *Harling 313* (S); Babahoyo-Montalve, *Sparre 14556* (S), *Cornejo & Bonifaz 4828* (GUAY, MO); Centro Cientifico Río Palenque, *Croat 38669* (MO, QCNE), *Dodson & Tan 5338* (SEL), *Croat 73826* (MO, QCNE), *Croat 50655* (MO), *Fallen & Ray 860* (SEL); Quevedo, *Asplund 15574* (S), *Dodson 6188* (RPSC, SEL); Vinces, Mocachi-Palenque, Jauneche forest, km 70 Quevedo-Palenque, via Mocachi, *Dodson et al. 10594* (GUAY, MO, SEL). **Manabí:** Portoviejo–Pichincha rd., ca. 20 km E of San Plácido, *Harling & Andersson 24778* (GB, MO); Cerro Montecristo, S of Manta, *Sparre 19488* (S); Machalilla NP, zona de San Sebastian, *Gentry et al. 72496* (MO, QCNE); Chone-Santo Domingo Rd., ca. 20 km NNE of Flavio Alfaro, Montañas de Convento, *Harling & Andersson 18898* (GB); Hacienda Don Juan, 10 km NE of Jama, N of Río Don Juan, *Neill et al. 11683* (QCNE); 28 km S of Pedernales, 3.5 km SW of Camarones, *Delinks 452* (AAU, NY, MO). **Napo:** Auca, *Plowman 14121* (F). **Pastaza:** Coca-Río Tiguino, 85.8 km S of Coca, *Croat 72573* (MO). **Pichincha:** vic. Hotel Tinalandia, 9.6 km E of Santo Domingo de los Colorados, *Croat 55666* (GUAY, MO, QCA); Machachi-Santo Domingo, 19.3 km E of Alluriquín, *Thompson & Rawlins 1104* (MO); Centinela, Montañas de Ila, 12 km E of Patricia Pilar, *Løjtnant & Molau 15839* (AAU); Santo Domingo-Quevedo, Patricia Pilar, *Dodson et al. 14638* (MO, QCNE), *Gentry et al. 26709* (MO); vic. of Santo Domingo de Los Colorados, Peripa, SW of Santo Domingo, *Croat & Nuñez 82064* (MO, QCNE); Nanegalito–Pto. Quito Rd., km 113, ENDESA, 5 km W of San Vincente Andoas, *Croat 82829* (MO), *Croat et al. 83795* (MO); Río Silanche, Quito-Pto. Quito, km 113, *Rodríguez 262* (NY, QCA); Santo Domingo–Quininde rd., km 41, *Zak et al. 5414* (QCA); vic. Maquipuquna Res., rd. to Maquipucuna Lodge, *Leimbeck R. 306* (AAU). **Sucumbios:** Lago Agrio-Baeza, ca. km 107, *Croat 50480* (MO). VENEZUELA. Maiquetia, *Andre 457* (K).

Cultivated specimens. Ecuador. Napo: Auca Oil Field, 23 Sep. 1991, *Ingram 1124* (MO).

16. Dieffenbachia longispatha Engl. & K. Krause, Pflanzenr. IV, 23 Dc(Heft 64): 44. 1915. TYPE: Panama. Colón: Fato (Nombre de Dios), July 1911, *H. F. Pittier 3838* (holotype, US!; isotypes, B!, F!, MO!). Figures 16, 29B.

Terrestrial, (1)1.5–3.5 m tall; sap very foul and pungent; stem prostrate at base, then erect; *internodes* 4–12 cm diam., with leaf scars prominent, dark green, semiglossy, drying dark brown to orange-brown; *petioles* thick and succulent, semiglossy, usually solid dark green, rarely streaked with pale green, 23–55 cm long (averaging 36 cm long), sheathed to about middle (0.58–0.85 their length, averaging 0.72); sheath 25–41 cm long (averaging 25 cm long), inequilaterally rounded at apex, sometimes weakly free-ending; unsheathed portion 4.0–30.5 cm long (averaging about 11 cm), C-shaped and obtusely sulcate or ± terete with a faint flat rib adaxially; *blades* oblong-elliptic, 41–72 × 17–38 cm (averaging 53 × 24 cm), 1.7–2.9 times longer than wide (averaging 2.3 times longer than wide), 1–2 times longer than petioles, coriaceous to subcoriaceous, semiglossy, bicolorous, weakly inequilateral, one side 0.6–3.5 cm wider than the other, usually short-acuminate at apex, sometimes acute to rounded with a short acumen, acute to rounded at base, with the edges turned up near the base; upper surface dark green, drying gray-green to dark olive-green, rarely yellowish brown; lower surface slightly paler, drying yellowish green, rarely yellowish brown; *midrib* flat, 1–2 cm wide at base, concolorous or slightly paler than surface above, drying slightly paler than surface and weakly raised above, concave to prominently raised on lower surface, drying brownish; *primary lateral veins* 15 to 26 pairs, sunken above, convex below, arising at an acute angle to the midrib then spreading at an angle of 45°–60°(70°), sometimes to 90° near the base of the blade, sometimes drying moderately wrinkled; interprimary veins lacking or 1 between each pair of primary lateral veins, sometimes almost as prominent as the primary lateral veins; minor veins indistinct. Juvenile blades with acute base and solid green midrib. INFLORESCENCES 1 to 3 per axil; *peduncles* (5.5)7–25 × 1.5–2 cm; *spathe* medium to dark green, broadly curved, long-acuminate, 27–48 cm long, 2.5–8.2 times longer than peduncle, to 4 cm wide at anthesis, tube flattening 5–12.5 cm wide, constricted area 2.5–3 cm diam., flattening 3.2–5 cm wide, spathe blade 3–6 cm wide at anthesis, flattening to 6–12 cm wide midway, the distal inner surface sometimes white when open; *spadix* (21)35–38 cm long; free portion 12–19 cm long; pistillate portion of spadix (except sometimes the uppermost part) fused to spathe, 13–15 cm long; fertile staminate portion (8)11–14 cm × (9)12–14 mm (drying 6–9 mm diam.); mostly sterile intermediate portion (2)3–4.3 cm long with a few scattered staminodia in the upper half (sometimes to throughout its length); pistillate flowers 10 to 26, round or barely bilobed, widely spaced, 5–10(20) mm apart, forming in a single irregular row or scattered but usually no more than 2 flowers across the width of the spadix (rarely 3); ovaries pale green, 4–7 mm diam.; stigmas 4–6 mm diam., yellow to orange, somewhat broadly bowl-shaped, 5–7 mm thick on the edge, medially with 1 to 2 somewhat elongate lobes, the lobes 1–1.5 mm diam., somewhat longer than broad; staminodia 5 to 6 per pistil, white, irregular, 2–6 × 2–3 mm, much flattened at base, less so toward the apex, often somewhat puckered at the apex; synandria in spirals of 4 to 7 each, 3–4 mm wide, subrounded, drying light yellow-brown and concave at apex. INFRUCTESCENCES 17–24 cm long; *berries* 1.5–2 cm diam., often deeply emarginate at both ends and

Figure 16. *Dieffenbachia longispatha*. —A. Habit with open inflorescence. —B. Plant habit with cluster of inflorescences. —C. Crown of plant with close-up of leaf base with open inflorescence. —D. Inflorescence at anthesis with staminate spadix exposed. A, C. (*Croat & Zhu 76257*); B, D. (*Croat & Zhu 76203*).

appearing to be a double fruit, bright yellow to orange; mesocarp ca. 2 mm thick, soft, sweet and tasty at maturity; seeds oblong, 7–8 mm diam., brown to black, smooth.

Distribution and habitat. *Dieffenbachia longispatha* ranges from central Panama to northern Colombia, mostly from sea level to 180 m, but perhaps to 250 m (owing to a collection at Río Tuquesa with no elevation reported), occurring in *Tropical moist* (T-mf), *Premontane wet* (P-wf), and *Tropical wet forest* (T-wf) life zones (Holdridge, 1967). In Panama it occurs on both coasts, but it is relatively rare on the Pacific slope.

Phenology. While collections of *D. longispatha* have been made in both flower and fruit year-round, flowering occurs principally during the first half of the rainy season between June and August, while fruits mature throughout much of the dry season and the first half of the rainy season, especially from February to September.

Discussion. *Dieffenbachia longispatha* grows most frequently along streams, in deposits of sediment along lakes, in standing water, but also in deep soil in the forest understory. Frequently it is found solitary or in small clusters. While the species may colonize, it is typically much less colonial than other species in Panama and Colombia, such as *D. isthmia*, *D. oerstedii*, or *D. killipii*.

The species is characterized by its usually tall ((1)1.5–3.5 m high) and robust stem (usually 6–12 cm diam.), and by the petiole being inconspicuously sheathed and decurrent at the apex with a long subterete free portion beneath the blade, this drying characteristically olive-green or dark brown. Perhaps most characteristic of *D. longispatha* are the widely scattered, moderately sparse and very large pistils and the usually long spathe. *Dieffenbachia longispatha* is typically one of the tallest species (to 3.5 m) with the thickest stems (to 12 cm diam.) in Central America. Only some plants of *D. panamensis* and *D. aurantiaca* often develop plants of comparable stature, but one collection of *D. standleyi* (*Madison 705*), with stems to 2.2 m tall and 9–11 cm diam., is reported.

The species has long been confused with *D. nitidipetiolata*, which ranges from Nicaragua to Ecuador. That species differs in having a typically somewhat smaller stature (usually 1–1.5 m tall), petioles that are in general very glossy, and pistils that are moderately small (to 3 mm) and closely aggregated. *Dieffenbachia nitidipetiolata* also has a different beetle pollinator scent at time of flowering according to observations made at La Selva in Heredia Province, Costa Rica, by D. Beath (pers. comm.). *Dieffenbachia longispatha* and *D. nitidipetiolata* do not occur together in Costa Rica since *D. longispatha* barely crosses west of the Panama Canal. In eastern Panama *D. longispatha* is found principally in areas of *Tropical moist forest* (T-mf) near El Real.

Smaller plants of *D. longispatha* may also be confused with *D. crebripistillata*. In addition to being a plant of smaller stature (rarely to 1.3 m tall), it has more fully sheathed petioles (often to the base of the blade and sometimes overlapping the blade) that usually have a whitish band abaxially and dry conspicuously yellow or orange-brown (vs. green for *D. longispatha*). In addition, *D. crebripistillata* differs in having smaller spathes (to 28 cm) with the pistils closely aggregated on the spadix, with (57)80 to 100 pistils versus 10 to 26 for *D. longispatha*. Finally, though there may be a certain overlap in their ranges in areas along the Atlantic coast in Colón Province, *D. crebripistillata* generally occurs at higher elevations, mostly 250 to 975 m.

Additional specimens examined. PANAMA. **Bocas del Toro:** 1.5 km N of La Gruta, *Peterson 6405* (US). **Canal Area:** Barro Colorado Island, Armour Trail 2000, *Croat 11321* (F, MO, US); Barbour Trail 225, *Croat 6471* (MO); Barbour Trail 200, *Croat 7136* (MO); Drayton Trail, near end, *Croat 5767* (MO); Drayton Trail 1610, *Croat 5761* (MO); Lake Trail, *Croat 6276* (MO, SCZ); *Oppenheimer 67-1-3-1244* (MO); Miller Trail 300, *Croat 4095* (MO); Miller trail 1400, *Croat 17394A* (MO); Miller Trail 1375, *Croat 7455* (MO); Pearson Trail 400, *Croat 4134* (MO); Snyder-Molino Trail, *Croat 6192* (MO); Van Tyne Trail, *Stimson 5277* (DUKE, STRI); Wheeler Trail 300, *Croat 4125* (MO); Zetek Trail 500, Fuertes Cove, *Croat 5259* (MO), *Croat 6409* (MO); 0.6 mi. N of Gamboa near Río Frijol, *Tyson 1438* (MO); vic. Curundu Housing area of Albrook Air Force base, Parque Metropolitano, *Croat & Zhu 76203* (AAU, CR, MO, US); Gatun Locks-Fort Sherman, 1 mi. E of Fort Sherman, *Croat & Zhu 76266* (MO, US); Río Grande-Pedro Vidal, rd. to Arraijan, *Pittier 2715* (US); near Fort Randolph, *Standley 28732* (US); Madden Forest ca. 3 mi. from Madden Wye, *Croat 33018* (MO, P, PMA); N of Summit Garden, *Croat 12319* (MO, US); Río Casaya headwaters, 6 km E of Gamboa, *Nee 9023* (F, MO). **Colón:** Río Guanche, Puerto Pilón-Portobelo, 6 km S of Portobelo, ca. 1.5 mi. S of rd., *Croat & Zhu 76256* (COL, MO, PMA, RSA), *76257* (COL, HUA, MO, PMA); Río Guanche, 1 km upstream, *Croat 75195* (MO), *Croat 11411* (MO). **Darién:** PN Cerro Pirre, vic. of station along Río Perisenico, *Croat & Zhu 77101* (CM, STRI, US); tributary of Río Tuira, upstream from El Real, *McDade s.n.* (MO); PN Darién, Cerro Pirre base camp, Río Paracida, *Croat 68971* (MO); 3 mi. E of Santa Fe, *Tyson et al. 4701* (US); Río Tuquesa headwaters, ca. 2 km air distance from Cont. Divide, Kittridge gold mining camp, *Croat 27196* (MO); Upper Río Tuquesa, *LeClezio 135a* (MO). **Panamá:** 5 mi. above Interam. Hwy., rd. to Cerro Azul, *Croat 11514* (MO, SCZ); El Valle de Madroño-La Saena, 2.5 mi. N of El Valle de Madroño, *Croat & Zhu 77042* (L, MEXU, MO); 5 mi. W of Chepo, *Tyson 6700* (MO); Río Majo-Quebrada Brava, *Croat 34654* (MO); El

Llano–Cartí Rd., near border with San Blas Province, *Croat 67399A* (MO); Río Tapia, *Standley 26156* (US), *Standley 28238* (US). **San Blas:** E of Puerto Obaldía, *Croat 16923* (MO). COLOMBIA. **Antioquia:** San Luis, *Guillermo & Cardenas L. 863* (HUA, JAUM). **Chocó:** Acandí, Río Cuti, Corr. Unguia, *Romero-Castaneda 6436* (COL); Nuquí, Corr. Arusí, vic. Arusí, Río Arusí, *Croat & M. Mora 83777* (= *Mora 394*) (MO). **Meta:** PN Natural Tinigua, Serranía Chamusa, Centro de Investigaciones Primatológicas La Macarena, Camp Colombia, *Stevenson 379* (COL).

17. Dieffenbachia lutheri Croat, sp. nov. TYPE: Panama. Chiriquí: along border of Bocas del Toro Province, Cerro Colorado, above mine, 1600 m, originally collected by *Luther et al.*, cultivated at Marie Selby Botanical Gardens (acc. #86-0873), 4 Oct. 1991, *S. W. Ingram 1146* (holotype, MO-4224350!; isotypes, B!, COL!, K!, MEXU!, PMA!, SEL-065912!, US!). Figures 17, 27B.

Planta 0.6–1.5 m alta; internodia brevia, 2.0–2.4 cm diam.; petiolus 23 cm longus, vaginatus 0.7 longitudinis; lamina anguste ovata, (24)27–34 cm longa, 14–15 cm lata, nervis primariis lateralibus 14–16 utroque; inflorescentia 1 per axillam; pedunculus 4–6 cm longus, 1 cm diam.; spatha pallide viridis, 16.5–20.5 cm longa.

Herb, 0.6–1.5 m tall; sap not smelling of oxalic acid; *internodes* short, to 2 cm long, 2.0–2.4 cm diam., dark green and semiglossy, drying matte and blackened; *petioles* ca. 23 cm long, dark green and weakly glossy, smooth or with fine, obscure lines on fresh material, sheathed 0.7 their length, drying dark olive-gray toward base, somewhat yellowish brown toward apex; sheath acute on one side at apex, the other side narrowly rounded at apex, with both sides confluent, the sheath margins drying thin, pale brown, the inner surface of the sheath pale yellow-green and very glossy, drying light yellow-brown, much paler than the outer surface; free portion of the petiole oval to sharply C-shaped in cross section, 7 cm long, sharply sulcate to flattened with sharply ridged margins; *blades* narrowly ovate, (24)27–34 × 14–15 cm, 1.9–2.2(2.7) times longer than wide, slightly inequilateral, one side 0.9–1.7 cm wider than the other, weakly to narrowly acuminate to acute and apiculate at apex, rounded and usually inequilateral, sometimes acute and decurrent on the petiole at base, moderately undulate along the margins, moderately coriaceous to subcoriaceous, very dark green and semiglossy to weakly glossy above, sometimes mottled in a band along the midrib (especially heavy on one side below the middle) with yellow-green to cream above, drying dark gray-brown to dark brown and matte to weakly glossy above, slightly to moderately paler and weakly glossy to matte below, drying yellow-green, weakly glossy; *midrib* slightly flat-raised, concolorous and 4–5 mm wide, weakly ribbed and medially sulcate above, narrowly rounded and slightly paler below, drying flat-raised and slightly darker yellow-brown above; *primary lateral veins* 14 to 16 per side, arising at an acute angle, then spreading at 25°–70° angle (25°–45° angle toward the apex, 65°–70° toward the base), weakly quilted-sunken to narrowly sunken and concolorous, sometimes in weak valleys above, darker and convex to round-raised, minutely granular-puberulent to scabridulous below, drying weakly and narrowly raised, concolorous above, irregularly angular and yellow-brown below; minor veins on upper surface in part weakly etched, concolorous, those on the lower surface moderately obscure to easily visible, darker than surface; lower surface densely pale-spotted, the spots regularly rounded and evenly spaced. INFLORESCENCE 1 per axil; *peduncle* 4–6 cm long, 1 cm diam., drying dark yellow-brown, 3.5–8 mm wide; *spathe* pale green on both surfaces, white near tip, acuminate at apex, 16.5–20.5 cm long, flattened to 3.5 cm wide on tube, drying yellowish brown; *spadix* 14–20 cm long (including 1–1.5 cm long stipe); pistillate portion of spadix 7.0–7.3 cm × 8–9 mm, completely contiguous with staminate portion or nearly so; staminate portion of spadix 5.3–8 cm × 5–9 mm on drying, with the remnants of thickened thecae visible along upper margins; pistils 55 to 66, 2 to 4 of them in a spiral across the width of the spadix, sometimes moderately sparsely spaced, drying sometimes prominently convex and the pistils thus visible from both top and side views; pistils 1.4–2.3 mm wide; stigmas pale yellow, 1.3–1.7 mm diam., drying with short, mostly acute, mostly erect strigose trichomes; staminodia 2–3 mm long, 1.0–1.6 mm wide, markedly thickened at the apex, sometimes broader than long, white, drying yellow-brown; synandria creamy white, drying irregularly rounded to angular, 0.5–3.0 mm wide, yellow-brown, the apex sunken on drying, medium yellow-brown with pale, rounded, cellular inclusions. *Berries* not seen.

Distribution and habitat. *Dieffenbachia lutheri* is apparently endemic to the region of Cerro Colorado in Chiriquí and Bocas del Toro Provinces at 1390 to 1600 m in the *Lower montane rain forest* (LM-rf) life zone (Holdridge, 1967).

Phenology. A flowering collection was made in Panama, and the species has flowered in cultivation in October at the Marie Selby Botanical Gardens.

Discussion. The species is most similar to *D. longispatha* in having a considerable portion of the petiole unsheathed and obtusely sulcate; the sheath

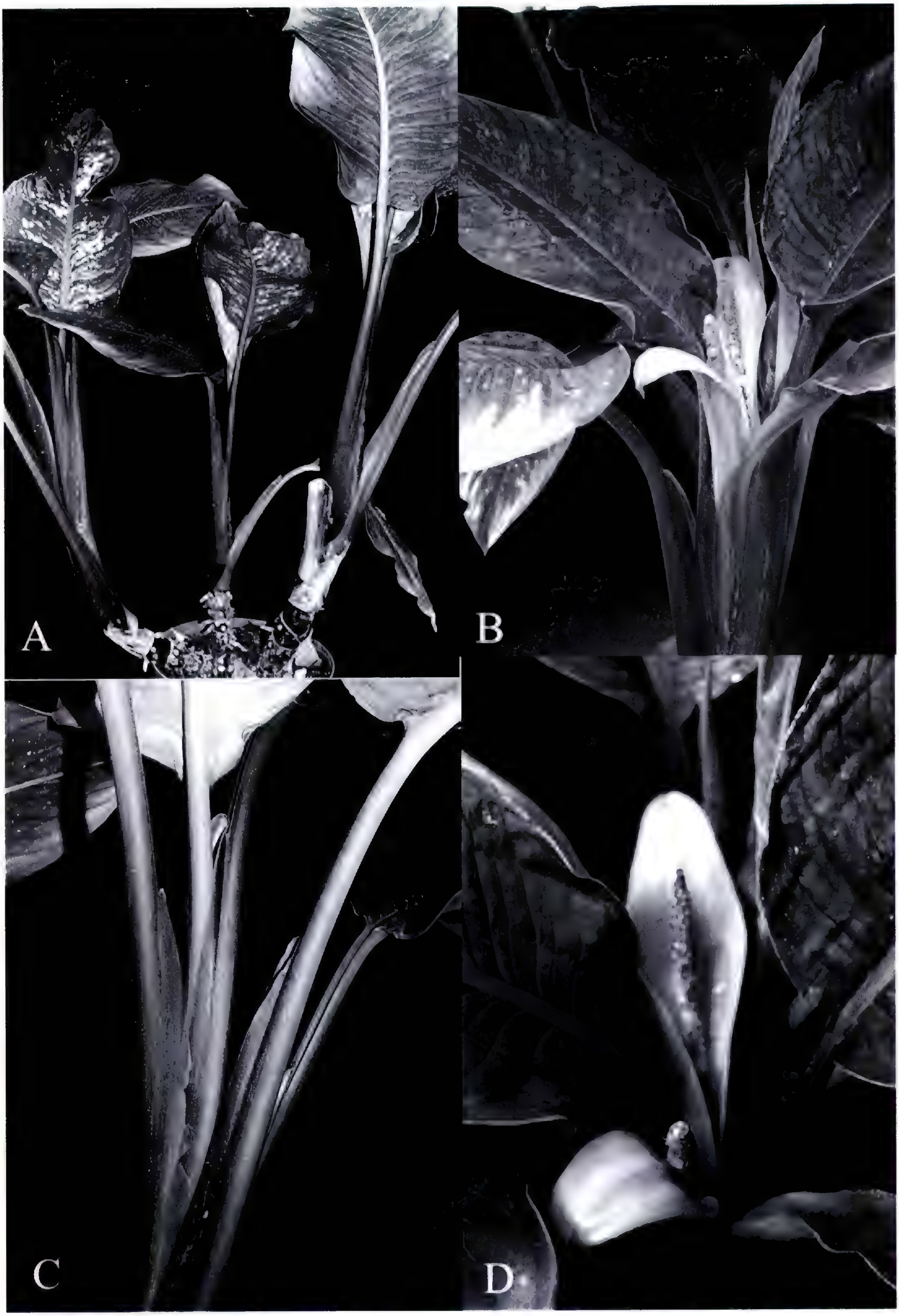


Figure 17. *Dieffenbachia lutheri.* —A. Habit of potted plant. —B. Plant habit with inflorescence. —C. Close-up of stem showing petiole sheath and sulcate petioles. —D. Close-up of inflorescence.

acute at the apex; and a blade of generally similar shape and dried color. It differs from *D. longispatha* in occurring at a much higher elevation (1390–1600 m vs. 180 m), in having the staminate and pistillate portions of the spadix contiguous (separated by a conspicuous, mostly sterile portion in *D. longispatha*), and in having a spathe that is much shorter (to 20.5 cm vs. 27–48 cm).

Dieffenbachia lutheri is also similar to *D. killipii* and even shares with that species the contiguous pistillate and staminate portions of the spadix. It differs from *D. killipii,* however, in having the major veins on the lower surface granular-puberulent rather than glabrous.

Dieffenbachia lutheri might be confused with another high-elevation species, *D. crebripistillata,* but that species occurs only up to 950 m, lower than *D. lutheri,* and differs in having a fully sheathed petiole that dries yellow-brown. *Dieffenbachia lutheri* has a petiole that dries dark gray and is unsheathed for more than 5 cm at apex.

Etymology. The species is named in honor of botanist Harry Luther from the Marie Selby Botanical Gardens, Sarasota, Florida, who collected living material of the type species.

Paratypes. PANAMA. **Bocas del Toro:** Cerro Colorado, 9.2 mi. W of Chamé, *Croat 69070* (MO). **Chiriquí:** Cerro Colorado, 18.6 mi. N of Río San Felix, 6.6 mi. beyond Chame, *Croat 75007* MO); 34.1 km of Río San Felix, *Croat 37268* (MO).

18. Dieffenbachia nitidipetiolata Croat & Grayum, sp. nov. TYPE: Panama. Bocas del Toro: Valle del Silencio, along Río Changuinola, ca. 1 km above mouth of Río Teribe, vic. Teribe Indian population, disturbed forest among cocoa plantations, 9°21′40″N, 82°31′40″W, 100 m, 25 June 1994, *T. B. Croat & G. Zhu 76449* (holotype, MO-04614032–33!; isotypes, AAU!, B!, CAS!, COL!, CR!, F!, GH!, INB!, K!, MEXU!, NY!, PMA!, US!). Figures 18, 30A.

Planta 50–75(120) cm alta; internodia 0.7–1.5 cm longa, 1.5–2.5(4.0) cm diam.; petiolus 13–44 cm longus, vaginatus 0.3–0.76 longitudinis; vagina 14–34 cm longa, acuta ad apicem; pars libera 5–22 cm longa; lamina oblongo-elliptica vel oblongo-lanceolata vel ovato-elliptica, 19–59 cm longa, 7–27.5 cm lata, nervis primariis lateralibus (10)12–20(22) utroque; inflorescentia 1–5 in quoque axilla; pedunculus 11–18(24) cm longus; spatha 15–36 cm longa; spadix 13–29 cm longus; pistilla 48–60(79).

Herb, 50–75(120) cm tall; sap moderately foul-smelling; stems erect or partially reclining; *internodes* 0.7–1.5 cm long, 1.5–2.5(4.0) cm diam., glossy to semiglossy, dark green to medium green, smooth, drying dark brown to light yellow-brown, matte, moderately smooth; petiole scars 4–5 mm thick. LEAVES erect-spreading, clustered at apex of stem; *petioles* 13–44 cm long (averaging 28.4 cm long), 1–1.5 cm diam. midway, sheathed 0.3–0.76 their length (averaging 0.48), very glossy as if varnished, rarely only semiglossy, dark green, drying orange-brown to blackened; sheath 14–34 cm long (averaging 14.3 cm long), erect to involute, acute and decurrent (but sometimes weakly elevated) at apex; the unsheathed portion 5–22 cm long (averaging 13.4 cm long), usually terete to C-shaped, sometimes obtusely and narrowly to broadly sulcate or V-sulcate, rarely D-shaped; *blades* oblong-elliptic to oblong-lanceolate, or ovate-elliptic, gradually acuminate to acute, equilateral to inequilateral at apex, usually only weakly inequilateral with one side 0.3–1.5 cm wider (but can be up to 3.5 cm wider) than the other, acute to obtuse or rounded at base, usually equilateral, sometimes inequilateral with one side acute and the other rounded, 19–59 × 7–27.5 cm (averaging 38 × 12.6 cm), 2.1–4.8 times longer than wide, broadest usually at middle, 0.7–2.4 times longer than petiole (averaging 1.38 times longer than petiole), subcoriaceous to thinly coriaceous, moderately to weakly bicolorous; margin sometimes weakly undulate; upper surface dark green and glossy to semiglossy, plain green or rarely weakly variegated with pale green in some areas or throughout much of the blade, sometimes plain green with just the midrib whitened, drying gray-green; lower surface moderately paler, matte to weakly glossy, drying yellow-green; *midrib* ± flattened (slightly sunken toward base), concolorous or slightly paler, sometimes white above, convex or bluntly acute below, drying pale yellow-brown often with a medial ridge on drying; *primary lateral veins* (10)12 to 20(22) per side, departing midrib at 20°–40°(55°) angle on narrower leaves (especially in Panama), often to 70°–85° angle on broader blades (mostly in Costa Rica), weakly arcuate-ascending, weakly sunken above, weakly convex and slightly paler below; minor veins visible, not prominent below. INFLORESCENCES mostly 1 to 5 per axil; bracts 2-ribbed throughout; *peduncles* 11–18(24) cm long, 0.9–1.3 cm diam., somewhat flattened, medium green, semiglossy; *spathe* 15–36 cm long, 1.3–2 times longer than peduncle, uniformly pale green to greenish white or greenish cream, becoming pale yellow post-anthesis, semiglossy to matte outside, slightly paler and glossy within, spathe tube 2–2.9 cm diam., flattening to 8–9 cm wide, weakly constricted above the tube to 1.7 cm diam., the constricted area to 5 cm wide when flattened, narrowly acuminate at apex; spathe blade 2.5–3.5 cm wide at anthesis, flatten-

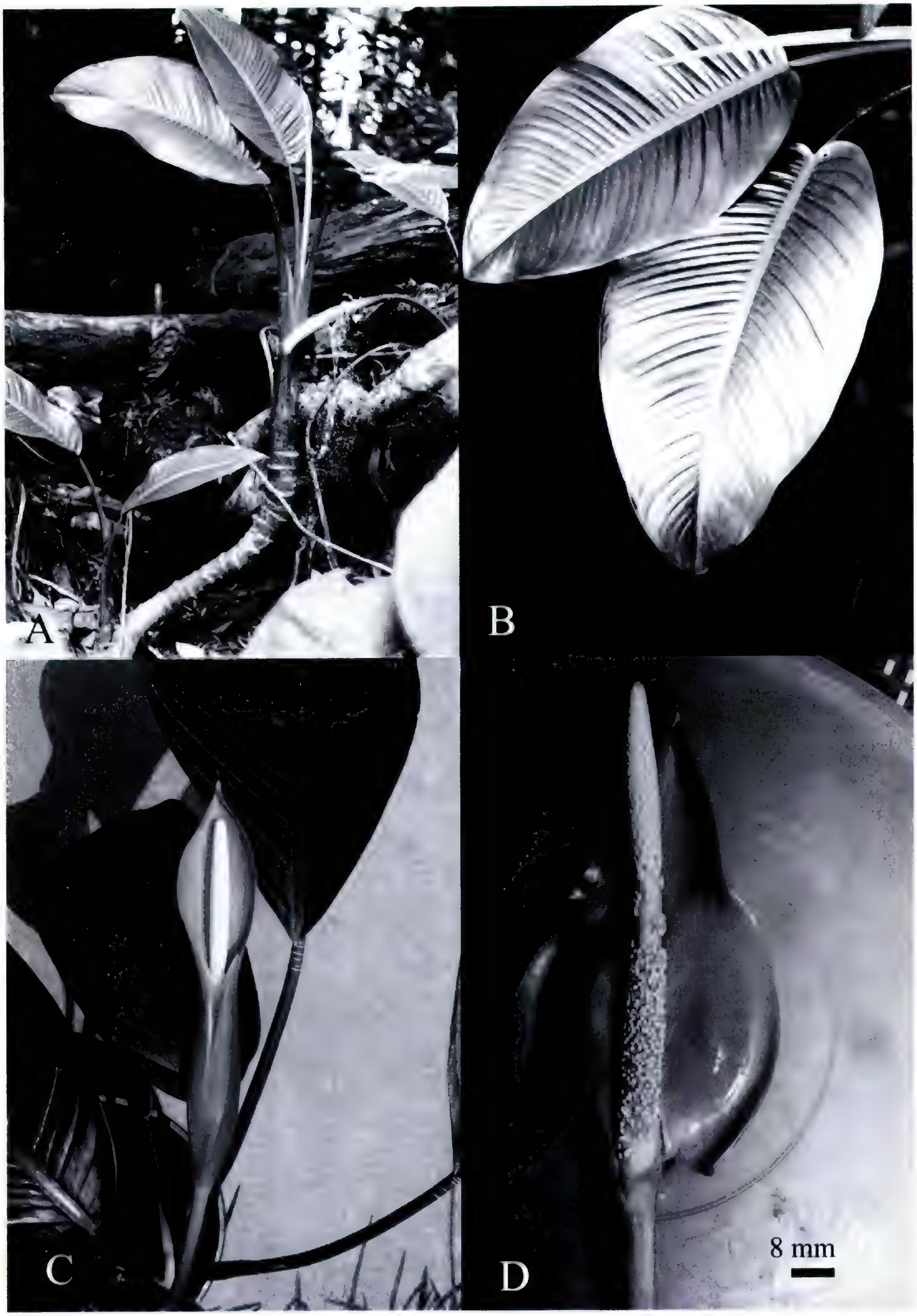


Figure 18. *Dieffenbachia nitidipetiolata*. —A. Habit. —B. Close-up of leaves, adaxial surface. —C. Close-up of crown of plant showing newly opened leaf and inflorescence. —D. Opened inflorescence exposing spadix. A, B. (*Grayum 3218*); C, D. (*Croat 76942*).

ing to (3.7)4.5–5.7 cm wide midway; *spadix* 13–29 cm long, ca. 1–9 cm shorter than the spathe; the free portion 11–16 cm long; fertile staminate portion 5.7–10.5 cm × 6–11 mm, slightly broader at middle, gradually tapering toward both ends, bluntly rounded at apex; male flowers 4 to 6 per spiral, subrounded to hexagonal, sometimes depressed medially, the margins irregularly and smoothly indented; pistillate portion 5.5–14 cm long, 11–15 mm diam., extending down to the very base of the spathe; pistils 48 to 60(79) globose, green, to 2.5–3 mm diam., moderately closely spaced except sometimes in uppermost 1 cm (the distance between them generally equaling or up to twice their width), usually to 3 per spiral or 4 to 6 in an arch across the width of the spadix; stigma yellow, depressed-globose, simple; staminodia 3 to 5 per flower, clavate, white, 2–6 mm long, up to 2 times longer than pistil, somewhat flattened and mostly contiguous at base (sometimes united in pairs), sometimes slightly thickened and somewhat puckered at apex, drying orange; staminate portion interrupted from pistillate portion by a ± naked portion, 2.5–4.5 cm × 5–9 mm with a few sterile staminate flowers scattered at both ends or sparsely in the lower half. INFRUCTESCENCES with spathe orange, to 23 cm long; *berries* globose, bright red, 4–6 mm diam.

Distribution and habitat. *Dieffenbachia nitidipetiolata* ranges from Nicaragua to Costa Rica (Heredia, Limón) to Panama (Bocas del Toro, Colón, San Blas), Colombia (Antioquia, Chocó), and Ecuador (Esmeraldas and Morona-Santiago), from near sea level to 1200 m in wetter parts of *Tropical moist forest* (T-mf), *Premontane wet forest* (P-wf), *Tropical wet forest* (T-wf), and *Premontane rain forest* (P-rf) life zones (Holdridge, 1967).

Phenology. *Dieffenbachia nitidipetiolata* flowers principally at the beginning of the rainy season (June–September), but also as early as March and as late as October, with the heaviest flowering apparently in August. Fruiting collections have been made from May through January.

Discussion. The species is characterized by its long, glossy petioles with the unsheathed portion being moderately elongate, 0.7–0.24 cm of their length, and which dry glossy as though varnished, and by the moderately closely spaced pistils. It is most easily confused with *D. longispatha*, differing from that species in having the pistils much smaller and aggregated and from *D. crebripistillata* in having the petiole almost unsheathed (vs. sheathed mostly to the apex in *D. crebripistillata*). The species may be confused with *D. hammelii*. That species differs in having a minutely granular upper surface, a matte-drying lower midrib with prominent raphide cells (vs. drying glossy without raphide cells), and matte-drying petioles (vs. drying glossy).

In the Río Guanche area of Colón Province, Panama, the species may be hybridizing with *D. crebripistillata* since both species occur along the Río Guanche and in the Santa Rita area further inland and at higher elevations. Some plants have the free portion of the petiole over half its length on average, which is characteristic of *D. nitidipetiolata* (but not of *D. crebripistillata*), yet the free portion is not notably glossy as is usually the case for *D. nitidipetiolata*. Examples of these collections are *McPherson & Merello 8235* from Santa Rita Ridge and *Thompson 4874* from Río Guanche. The McPherson and Merello collection also describes the petiole as having a white streak on the abaxial surface, a feature otherwise known only in *D. crebripistillata*.

Paratypes. COSTA RICA. **Alajuela:** 34 km beyond San Ramón beyond Los Angeles, *Luteyn 3385* (DUKE); 3.5 km W of Fortuna, 2.5 km NW of New Volcán Arenal, *Taylor & Taylor 11660* (MO); Naranjo-Aguas Zarcas, along Hwy. 15, 8 km NE of Quesada, *Croat 46947* (MEXU, MO); N side of Volcán Arenal, *Lent et al. 3374* (F); Cordillera de Tilarán, San Ramón-Bajo Rodríguez, 36–37 km NW of San Ramón, *Croat 68195* (CM, K, MO); 15 km WNW of Quesada by air 1 km W of Jabillos, *Liesner et al. 15144* (B, CR, MO, WIS); Río San Lorenzo, San Lorenzo-Los Angeles de San Ramón, *Burger & Antonio 11198* (F, MO); Río San Rafael, W of La Marina, *Burger & Stolze 5024* (F, US). **Cartago:** Turrialba-Limón, Hwy. 32, ca. 9 mi. NE of Turrialba, *Croat 43368* (MO); Guacimo–Guapiles Rd., *Barringer 2416* (F). **Heredia:** La Selva at Sarapiquí, *Jimenez 103* (MO); La Zona Protectora, Río Guacimo, *Grayum & Schatz 3218* (DUKE); La Selva, OTS Field Station on the Río Puerto Viejo, E of its jct. with the Río Sarapiquí, *Croat 44254* (MO), *Hammel 8123* (DUKE, F, MO), *Burger & Stolze 5753* (F, GH), *Folsom 9200* (DUKE), *Hammel 10082* (DUKE), *Beach 1436* (DUKE), *Beach 1439* (DUKE, MO), *MacDougal 1027* (DUKE), *Jiménez 103* (MO); Río Sarapiquí, 2 km S of San Miguel, *Lent 37* (F); Sarapiquí, *Croat 44307* (MO), *Grayum 2225* (DUKE, MO); San José and Pto. Viejo, vic. of Chilamante, 11.6 mi. N of Cariblanco, *Croat 68379* (MO). **Limón:** Hitoy Cerere reserve, SW of Valle La Estrella, along Río Cerere to ca. 1 km upstream from Quebrada Barrera, *Grayum & Hammel 5785* (MO); Res. Biol. Hitoy Cerere, Valle de la Estrella, trail to Cerro Bobócara, *G. Herrera 4116* (CR, MO); N of Quebrada El Molinete, Río Chirripó-Río Corinto, *Grayum & Jacobs 3524* (MO); Ref. Nac. Barra del Colorado, Río Chirripócito-Río Sardina, *Grayum 9844* (CR, MO); Río Catarata, *Burger et al. 10323* (F, MO, SEL); BriBri-Río Sixaola, Río Catarata, *Burger & Antonio 10905* (F, MO, PMA); BriBri-Caribbean coast, *Croat 43217* (MO). **Puntarenas:** E of Monteverde on the Pacific watershed, *Burger et al. 10699* (MO); Palmar Norte-Panamerican border, 3 km N of turn-off to Rincón, *Croat & D. Hannon 79199* (INB, MO, US). **San José:**

Vazquez de Coronado, Braulio Carrillo NP, along Hwy. San José to Siquirres, trail to Río Sucio, site of the Old Carillo Station, *Croat 78788* (IBE, INB, MO, WU). NICARAGUA. **Zelaya:** Caño Montecristo, E of Campamento Germán Pomares, *P. Moreno & J. Sandino 15160* (MO); Río Punta Gorda, Atlanta, "La Richard," 200 m SE, *Moreno & Sandino 12976* (MO). PANAMA. **Bocas del Toro:** Río San Pedro, *Gordon 55C* (MO); Santa Catalina, 4 Dec. 1967, *Blackwell et al. 2704* (COL, MO, UC); Chiriquí Lagoon area, Cocoa Cay, *von Wedel 2892* (COL, F, MO, UC); above RR stop at Milla 7.5, *Croat & Porter 16303* (MO), *Croat & Porter 16412* (MO), *Croat 38120* (HUA, INB, MO, UB, VEN), *Croat & Porter 16375* (MO); Chiriquí Grande-Fortuna, 7.7 mi. S of Chiriquí Grande, 1.5 m W of Punta Peña, *Croat & Grayum 60116* (MO), *Akers 78* (MO); IRHE vic., *Carrasquilla & Mendoza 1239* (MO, PMA); Almirante-Ojo de Agua, 3–6 km W of Almirante, *Croat 38229* (F, MO, PMA); about 10 mi. W of Veraguas border, *McPherson 11401* (CM, MO); Valle del Silencio, along Río Changuinola, ca. 1 km above mouth of Río Teribe, vic. Teribe Indian population, *Croat & Zhu 76422* (INB, MO, WU); Cocoa Cay, vic. of Chiriquí Lagoon, *von Wedel 2892* (F); Río Teribe, vic. Teribe II, IRHE, *Carrasquilla 2005* (PMA); Changuinola-Tuibe Rivers, Zigla Rd., *Lazor et al. 2578* (MO); limit trail of Par. Intl. La Amistad, from Quebrada Boca Chica to Quebrada Bonyic, *Polanco 1591* (PMA). **Chiriquí:** Fortuna Lake Area, 3.4 km N of Quebrada Chorro, 1.6 mi. N of center of bridge over lake, *Croat 74958* (MO); vic. Fortuna Dam, *McPherson 9829* (MO); Quebrada Los Chorros-Quebrada Hondo, N of Fortuna Lake, *Churchill & Churchill 6105* (MO); Fortuna-Chiriquí Grande, 0.7 mi. NW of center of dam, *Croat & Zhu 76482* (INB, MO, PMA); trail from rd. near Forestry Nursery to Río Hornito, *Thompson 5028* (CM). **Coclé:** Cont. Divide, N of Penonome on rd. to Coclesito, *Hammel 4049* (MO). **Colón:** Santa Rita Ridge rd., ca. 8 mi. E of Transisthmian Hwy., *McPherson & Merello 8235* (MO); Santa Rita Ridge Rd., ca. 1 hr. walk from end of rd., *Antonio 4488* (MO); Santa Rita Ridge Rd., 6.5 mi. E of Boyd-Roosevelt Hwy., *Croat & Zhu 76942* (CR, GOET, GUAT, HUA, INPA, ISC, LE, MO, PMA TEFH, UB, WISC); Puerto Pilón-Portobelo, Río Guanche, ca. 1.5 mi. S of rd., *Croat & Zhu 76254* (MO, PMA); Río Guanche, 3–5 km above bridge, *Croat 79348* (B, INB, MEXU, MO, US), *Sytsma 1695* (MO); 3–7 km above bridge, *Hammel et al. 4882* (MO); ca. 3 km above bridge, *Croat 49761* (MO); Santa Rita-Serra Llorona, *Galdames et al. 1138* (STRI); Río Iguanita, *Croat 49768* (MO). **Darién:** W side of Cerro Pirre, *Croat 68854* (MO); Río Tuquesa, ca. 2 km air distance from Cont. Divide, near upper gold mining camp of Tyler Kittredge, *Croat 27161* (MO); Serranía de Pirre, Río Cana-Río Escucha Ruido, above Cana Gold Mine, *Croat 37746* (MO). **Panamá:** El Llano–Cartí Rd., near border with Province of San Blas, *Croat 67379A* (MO). **San Blas:** Comarca de Kunayala, Nusigandí, El Llano–Cartí Rd., 10.1 mi. N of Inter-am. Hwy., then ca. 0.5 mi. N Paseo Mariska, *Croat & Zhu 77023* (MO); SE of Puerto Obaldía, *Croat 16769A* (MO); trail from dock to airport to village of Cangandí, *de Nevers et al. 7407* (MO, PMA); El Llano–Cartí Rd. km 16.7, trail W to waterfall 5 km from rd., *de Nevers & S. Charnley 5898* (MO, PMA); Canagangí, *de Nevers et al. 5727* (MO). **Veraguas:** Boca de Concepción, in Golfo de los Mosquitos, *McPherson 11381* (MO). COLOMBIA. **Antioquia:** Mutatá, Corr. Longani, *Callejas et al. 5661* (HUA). **Chocó:** trail from Río Mecana to Alto de Mecana, *Gentry & Juncosa 41037* (MO); Serranía de Baudo, Las Animas-Pato, Río Pato, 10 km SW of Pato, *Croat 56070* (CHOCO, MO); Río Condoto-Río San Juan, *Killip 35113* (COL, US); Alto de Buey, *Gentry & Forero 7342* (COL, MO); Bahia Solano, Puerto Mutis, *Gentry & Forero 7217* (COL, MO); Bahia Solano, *Croat 57462* (CHOCO, COL, MO); N of Bahia Solano, Cerro Mecana, *Juncosa 1795* (MO); Mecana, Quebrada Resaquita, *Juncosa 1898* (MO), *1912* (MO); Río San Juan, Noanama, *Forero et al. 4571* (COL); Río Bicordo, tributary of Río San Juan, Noanama, *Forero et al. 4659* (COL); Acandí, Quebrada Sardí, El Páramo, *Roldan et al. 1199* (HUA, MO); Corr. San Francisco, Vereda Coquital, sitio El Páramo, Quebrada Zardí, *Betancur et al. 1177* (HUA); Vereda Coquital, *Fonnegra et al. 2899* (HUA, NY), *2907* (HUA, NY); Nuquí, Corregimiento Arusí, vic. of Arusí, Est. Biol. El Amargal, *Croat & Mora 83652* (= *Mora 270*) (MO); Corr. Arusí, Est. Biol.. El Amargal, *Mora 170* (COL). ECUADOR. **Esmeraldas:** Zapallo Grande, Río Cayapa, *Barfod et al. 48348* (AAU); Lita-San Lorenzo Rd., 0.9 km E of El Durango, 19.8 km W of Alto Tambo, *Croat et al. 82520* (MO); Playa de Oro, 1 km from Río Santiago, *Cerón & J. Corozo 33858* (QAP), *33947* (QAP), *Cerón & J. Corozo 34097* (QAP); San Lorenzo-Mataje, departing main Lita–San Lorenzo Hwy., 11.6 km N of Gasolinera San Lorenzo, 2.9 km W of main Lita-San Lorenzo Hwy., *Croat et al. 84041* (AAU, B, CAS, COL, DUKE, G, K, M, MO, NY, P, UB, US, WU); Cotacachi Cayapas, San Miguel, Río Cayapas, Sector Loma Linda, *Tipaz et al. 2280* (MO, QCNE); Río Cayapa, Zapallo Grande, *Barfod et al. 48154* (AAU, MO); Zapallo Grande, *Kvist et al. 48348* (AAU, QCA); Río Cayapa, Zapallo Grande, *Kvist & Asanza 40756* (AAU); Río Grande, at Zapallo Grande, *Barfod & Skov 60101* (AAU); Río San Miguel, upstream from Pueblo Cayapas, *Holm-Nielsen et al. 25355* (AAU); San Lorenzo, *Sparre 18326* (S). **Morona-Santiago:** Santiago-Morona, Río Morona, 23.4 km E of Santiago, *Croat 87448* (MO, QCNE).

19. Dieffenbachia obscurinervia Croat, sp. nov. TYPE: Panama. San Blas: trail from dock to airport to village of Cangandí, 9°24′N, 79°24′W, 3–30 m, 26 Mar. 1986, *G. de Nevers, H. Herrera & S. Charnley 7409* (holotype, MO-3475792!; isotypes, B!, US!). Figures 19, 29A.

Planta 0.8–1.5 m; internodia brevia, (1)3–4(5) cm longa, 1.5–2.5(3) cm diam.; petiolus 8–12 cm longus, vaginatus ad medium vel ad apicem; lamina anguste elliptica, 20–30 cm longa, 5–8 cm lata; inflorescentia 1–3 per axillam; pedunculus (1.7)3–5 cm longus; spatha 11.5–20 cm longa; spadix 10–18 cm longa, cum parte pistillata 5–5.5 cm longa.

Slender herb, 0.8–1.5 m tall, stem decumbent on older parts, weakly rooted, leaf scars inconspicuous; *internodes* glossy, (1)3–4(5) cm long, 1.5–2.5(3) cm diam., dark green, epidermis fissured minutely into a netlike reticulum becoming uniformly fissured and brown-scurfy with age; *petioles* 8–12 cm long, averaging 10.6 cm long, sheathing ½ to throughout (average 0.8 their length), light green or yellow-green with the surface dark green-splotched or dark green with white or yellow spots (sometimes with spots forming a repeated series of irregular

Figure 19. *Dieffenbachia obscurinervia.* A, B. (*Croat 12660*). —A. Cluster of several potted plants with plant on left with open inflorescence. —B. Close-up of crown of plant showing adaxial and abaxial surfaces and inflorescence at anthesis. —C. Close-up of stem showing mottled epidermis and speckled petioles (*Croat 61234*). —D. Close-up of inflorescence showing both pistillate and staminate portions of spadix (*Croat 13849*).

bands); sheath 6.7–10 cm long, the tip usually rounded to inequilaterally emarginate, rarely decurrent, frequently with one side emarginate and with the other side acute; unsheathed portion lacking or to 5.2 cm long, sharply to bluntly sulcate; *blades* narrowly elliptic, 20–30 cm long (averaging 24 cm long), 5–8 cm wide (averaging 7.5 cm wide), 2.4–5.2 times longer than wide, 1.6–3.1 times longer than petiole, slightly inequilateral, one side 0.7–1 cm wider than the other side, subcoriaceous, weakly bicolorous, gradually acuminate, briefly apiculate at apex, frequently somewhat falcate, cuneate to obtuse or rounded, often weakly inequilateral, rarely weakly subcordate at base; upper surface dark green, semiglossy, drying dark yellow-green to dark olive-green; lower surface slightly to moderately paler, drying yellow-green; *midrib* slightly raised to flat above, concolorous, drying concolorous above, convex to narrowly rounded below, dark green, densely pale yellowish green-spotted, drying paler than surface or darker than surface below; *primary lateral veins* 10 to 13 per side, weakly etched above, weakly raised or not at all raised below; the interprimary veins almost as conspicuous as primary lateral veins; minor veins moderately distinct below. INFLORESCENCES 1 to 3 per axil; *peduncle* (1.7)3–5 cm long, somewhat flattened in cross section; *spathe* 11.5–20 cm long, 3.2–9.5 times longer than peduncle, dark green or pale green throughout, caudate-acuminate, sometimes sharply reflexed below apex; *spadix* 10–18 cm long; free portion 5–9 cm long; pistillate portion 5–5.5 cm long; sterile segment less than 1 cm long, 6 mm diam., with scattered staminodia throughout; pistils 20 to 40, moderately closely spaced, scattered, 2–2.6 mm diam.; stigma depressed-globose, 2 mm diam.; staminodia white, usually 3 per pistil, 1.5–2(3.4) mm long, flattened, oblong to clavate, grooved medially, drying flattened, thickened at apex; synandria irregularly rounded with margins undulate, minutely warty, widely sunken at apex, 1.8–2.6 mm diam., dark yellow-brown, matte on drying. INFRUCTESCENCE broadly arching; spathe mostly deciduous; spadix to 8 cm long; *berries* red, broadly ellipsoid, to 1.5 cm long, less than 1 cm diam.

Common name. Abior (Kuna) (*de Nevers et al. 7409*).

Distribution and habitat. *Dieffenbachia obscurinervia* ranges from central Panama (as far west as Coclé) to northern Colombia (Antioquia and Chocó) from 30 to 800 m in *Tropical moist forest* (T-mf) and *Tropical wet forest* (T-wf) life zones (Holdridge, 1967).

Phenology. The species has been seen in flower from May to December and fruiting collections have been reported from from September to May.

Discussion. *Dieffenbachia obscurinervia* is characterized by its scurfy brown internodes, conspicuously splotched petioles, and narrow blades with weakly developed primary lateral veins. It is not easily confused with any other species but was incorrectly called *D. pittieri*, a species considered restricted to the Isthmus of Panama, for many years. See that species for a discussion of the differences.

Paratypes. PANAMA. **Canal Area:** Pipeline Rd., mi. 1–3, N of Gamboa, *S. Knapp 1042* (MO); Pipeline Rd. at Río Agua Salud, *Croat 12352A* (MO); Barro Colorado Island, Armour Trail 1280, *Croat 8623* (MO); Drayton Trail 1000, *Croat 12660* (MO); Drayton 1910, *Croat 6775* (MO, STRI); Drayton 1490, *Croat 5759* (MO). **Coclé:** vic. El Valle de Antón, La Mesa, Finca Macarenita, *Croat & Zhu 76666A* (MO, PMA). **Colón:** Santa Rita Ridge, *Croat 13849* (MO); Nombre de Dios, *Croat 67329* (MO); Coclé del Norte, *Hammel 4484* (MO); Portobelo-Nombre de Dios, 1.2 mi. beyond jct. of rd. to Isla Grande, *Croat 49791* (MO, PMA); Río Guanche, ca. 5 km upstream from rd. to Portobelo, *Hammel & Trainer 14786* (MO); Loma de la Gloria, near Fato (Nombre de Dios), *Pittier 3847* (US). **Panamá:** Balboa West, *Zapata et al. 289* (PMA); along trail off Llano-Cartí Rd., 4.6 mi. from jct. with Pan-Am. Hwy., *McPherson & Merello 8143* (MO). **San Blas:** Río Cangandí, Cangandí, *H. Herrera 245* (MO, PMA); Nusigandí, along El Llano–Cartí Rd., 0.7 km beyond Cuna headquarters, 11.6 km from Pan-Am. Hwy., *Croat 75149* (K, MO). COLOMBIA. **Antioquia:** Río Anorí valley, near Planta Providencia, *Shepherd 438* (MO, WIS); Anorí, Corr. Prov., *Soejarto & Renteria 3556* (HUA); Zaragoza, Río Anorí, Quebrada La Tirana-Río Anorí, 2 km N of Quebrada La Tirana, 3 km upriver from Planta Providencia, *Alverson et al. 283* (COL); Carepa, Tulenapa Reserva (ICA), Turbo-Mutatá, 40 km S of Turbo, *Callejas et al. 4873* (MO, NY). **Chocó:** Nuquí, Quebrada Chaquí, *Galeano et al. 4825* (MO); Quibdó, La Concepción, 15 km E of Quibdó, *Archer 2215* (US); Cordoba, Tierralta, Río Esmeraldas-Río Simí, 2 km above confluence, *Bernal et al. 1158* (COL).

20. Dieffenbachia oerstedii Schott, Oesterr. Bot. Z. 8: 179. 1858. TYPE: Guatemala. Aguacate, *A. S. Oersted s.n.* (holotype, C!). Figures 20, 29A.

Herb, 30–75(100) cm tall (usually less than 50 cm); stem erect or partially reclining, often conspicuously clustered with numerous plants; sap

→

Figure 20. *Dieffenbachia oerstedii.* —A. Potted plant with inflorescences and leaves with mottled blades (*Croat 68449*). —B. Potted flowering plant with pale midribs (*Croat & Zhu 76794*). —C. Leaves and post-anthesis inflorescence showing ovate-lanceolate blades with scarcely sunken primary lateral veins (*Croat 63208A*). —D. Close-up of

Figure 20. (Continued) stems showing the free-ending petiole sheath (*Croat 36297*). E, F. (*Croat 68449*). —E. Flowering plant with open inflorescences. —F. Close-up of flowering plant showing open spathe blade and exposed staminate portion of inflorescences.

moderately foul; leaf scars conspicuous, transverse or oblique (when oblique, up to 2× as wide on one side as the other), forming a T or forming a W on open side of sheath; *internodes* semiglossy to glossy, weakly warty on magnification, 1–5.7 cm long, 0.8–2(3) cm diam., dark olive-green to blackish green, medium green or dark green, sometimes variegated with streaks of paler green, drying dark brown to dark yellow-brown, glossy, smooth; *petioles* 10–20(30) cm long, (averaging 13.7 cm long), 3–4 mm diam., sheathing ⅓ to ¾ (rarely nearly throughout) their length (averaging 0.7 their length), medium green, matte, sometimes finely streaked throughout with darker green, usually weakly glossy and white near base; sheath 2.5–21.5 cm long (averaging 9.3 cm long), pale green to white on lowermost clasping portion (contrasting sharply with much darker stem), with margins involute, the tip with one side erect, free-ending and rounded to auriculate, with the other side rounded to acute (sometimes not free-ending in Coclé Province, Panama); unsheathed portion 5–13 cm long, C-shaped to U-shaped in cross section, convex adaxially, acute to bluntly angled on margins; *blades* ovate to narrowly ovate or ovate-lanceolate or rarely oblanceolate, (5.5)14–22(35) × (1.7)4–14(21.5) cm, (averaging 20.1 × 8.5 cm), 1.4–5.9 times longer than wide (averaging 2.5 times longer than wide), 0.8–2.7 times longer than petiole (averaging 1.5), often inequilateral, somewhat thinly coriaceous to subcoriaceous, moderately bicolorous, gradually acuminate and apiculate at apex (the acumen 5 mm long), acute and weakly decurrent to obtuse or more often rounded, sometimes subcordate at base; upper surface matte and subvelvety to weakly glossy, dark green, frequently splotched light or medium green or with white areas especially near midrib (all variations frequently found in a single population), drying dark brown to gray-green, concolorous, sometimes faintly dark-striate; lower surface matte to weakly glossy (epidermal cells raised and sometimes translucent), drying yellow-green to yellow-brown, sometimes faintly dark-striate, slightly paler; *midrib* flat-raised to obtusely flat-raised above, concolorous or sometimes white above (sometimes mottled on plants with mottled leaves, sometimes faintly dark-striate on both surfaces), slightly paler and convex to broadly convex to bluntly acute below; *primary lateral veins* (4)6 to 9(11) per side, departing midrib at a 40°–45° angle, broadly arcuate-ascending, sunken to quilted-sunken above, slightly darker than surface, weakly convex-pleated below; interprimary veins weak or as conspicuous as primary lateral veins; minor veins indistinct above, moderately distinct to moderately obscure below; "cross-veins" sometimes visible. INFLORESCENCES 1 to 2 sometimes 3, rarely 4 per axil; *peduncle* (2.2)3.5–12(22) cm long (average 7.6 cm long), $\frac{1}{10}$ as long as spathe to fully as long as the spathe, averaging 0.43 as long, 6–13 mm diam., 2–4 mm diam. on drying, somewhat flattened in cross section; *spathe* (7.5)10–17(25.5) cm long, weakly constricted above tube, medium green on both surfaces, sometimes tinged whitish on back throughout (the median rib green), weakly glossy to semiglossy outside, glossy on inside, narrowly acuminate at apex; tube to 2–2.8 cm wide, 1.5–2.3 cm thick when furled, to 8 cm wide when flattened; spathe blade to 2.5 cm diam. when furled, 3.0–8 cm wide at anthesis; *spadix* (7)10–17(21) cm long (averaging 14.6 cm), 1–5 cm shorter than spathe; pistillate portion 4.3–7.5(10) cm long (averaging 6.4 cm long), 5–10 mm diam.; fertile staminate portion 3–8.5 cm long (averaging 5.3 cm long), 5–7 mm diam., broadest at middle, tapering toward both ends, especially at bluntly pointed apex; mostly sterile intermediate segment (1)2–3.2 cm long, to 2.5 mm diam. (dried), with a few widely scattered sterile staminate flowers in upper ¾ and a few pistillate flowers in lower ¼, sometimes with only sterile staminate flowers scattered throughout, rarely almost bare; pistils (26)33–46(54), moderately closely spaced except in the lower 1.5 cm and the upper 1 cm (the distance between them generally equaling or twice their width), up to 4 in a row across the width of the spadix, subglobose, 1.5 × 1.4–2.6 mm; stigma depressed-globose, yellow, 1 mm wide, puberulent; style caviform with a weak central dome; staminodia clavate, white, drying orange, 2–3(4.5) mm long, 1–2 mm wide at apex, 2–3 times longer than pistil, usually weakly fused at base, sometimes well separated, weakly flattened, thickened toward apex; synandria 3 to 5 per spiral, 1.4–2.0 mm diam., the margins smooth to irregularly and smoothly indented, smooth and subrounded at apex. INFRUCTESCENCE to 22 cm long; spathe orange outside; *berries* bright red, globose, with 13 to 43 per spadix, 4–6 mm diam.

Distribution and habitat. *Dieffenbachia oerstedii* ranges from Mexico (Veracruz, Oaxaca, Chiapas, and Tabasco) mostly along the Caribbean slope in Central America in Guatemala, Honduras, Nicaragua, and Costa Rica (where it occurs on both slopes) and west-central Panama. The species also occurs on the Pacific slope of El Salvador (Department of Ahuachapán). The species ranges from sea level to 1260 m in *Tropical dry* (T-df), *Tropical moist* (T-mf), *Tropical wet* (T-wf), *Premontane wet* (P-wf),

and *Premontane rain forest* (P-rf) life zones (Holdridge, 1967).

Phenology. Flowering of *D. oerstedii* occurs throughout the year, but with the heaviest flowering at the end of the dry season and the first part of the rainy season, April to September. Fruit maturation is more regularly scattered throughout the year.

Discussion. This species is characterized by its small stature (generally less than 1 m tall); frequently clustered stems; and sharply C-shaped petioles that are whitish at the base and sheathed mostly ⅓–¾ their length, with the sheath obscurely free-ending and inequilateral with at least one side usually merely rounded or acute rather than auriculate. Also characteristic are the moderately thin, usually small, ± ovate-lanceolate blades, which are generally acute to rounded or truncate basally and matte or only weakly glossy adaxially.

Dieffenbachia oerstedii is the most widespread and ecologically variable species in Central America. It is extremely malleable in terms of leaf size, leaf blade shape, and markings, with different blade coloration types (cf. Fig. 20A, B) all found within the same population. For example, in populations at Río Grande de Taracoles at Carara in Costa Rica (0–200 m), the plants of this species are robust. The populations of *D. oerstedii* at 1400 m in Braulio Carillo National Park (also Costa Rica) have small and delicate leaves. In Costa Rica, the leaf blades tend to be matte or only weakly glossy on the upper surface. However, elsewhere in Central America the blades are often more glossy. A collection from El Salvador (*Selby 77-3078*) has blades that are initially rather glossy on the upper surface and weakly glossy on the lower surface (albeit soon turning only weakly glossy above). Plants in Panama and Costa Rica have blades 2–11 cm wide and acute to rounded at the base, whereas in other parts of Central America from Nicaragua to Mexico the blades are often 14–18 cm wide with subcordate leaf bases.

Standley (1937) considered *Dieffenbachia leopoldii* (Bull. Catal. 1878) similar to or synonymous with *D. oerstedii*, but the type specimen indicates that it was actually collected in Colombia, where *D. oerstedii* does not range. The species is actually closer to *D. killipii* (see discussion under *D. killipii*).

Collections from Mexico and Belize are larger on average than those in Panama, Costa Rica, and Nicaragua, with blades 16.5–35 cm long and 6–16.5 cm wide (averaging 23 × 11 cm). Petioles for the same area range from 8.5 to 30 cm long, about as long as the blades to 1.7 times longer than the blade with the sheath from 7.5 to 21.5 cm long, averaging 14 cm long (sheathed 0.48–0.9 the petiole length). In contrast, plants from Heredia Province in Costa Rica are smaller than average with blades averaging 13.9 cm long and 5 cm wide (2.9 times longer than wide).

The distribution of *Dieffenbachia oerstedii* in Panama is apparently disjunct with some collections known from far western Panama, but the species also occurs in the vicinity of El Copé and La Mesa in Coclé Province. The populations in El Copé have somewhat smaller leaves (9.5–15 cm long), but differ only slightly from those in Costa Rica. The El Copé material is otherwise morphologically identical to populations of *D. oerstedii* such as those found at La Selva in northern Costa Rica.

The petiole sheath of the Coclé populations is merely rounded on one side and acute on the other (vs. auriculate on one side and rounded on the other side for typical material of *D. oerstedii*). In addition, the midrib is not faintly striate on both surfaces as is usually the case with typical *D. oerstedii*. The petiole scars are much more oblique than usual with the internodes longer on one side of the stem than on the other (vs. more nearly perpendicular to the stem with the internodes of equal width on both sides of the stem for typical *D. oerstedii*). Despite the strong morphological similarities, plants from Coclé Province, Panama, differ markedly in their ecological requirements. Cultivated plants, for example, will survive well only in an area of nearly 100% humidity. Alternatively, the Costa Rican material from Heredia does very well in the drier parts of the greenhouse.

In Mexico, *Dieffenbachia oerstedii* may be confused with *D. wendlandii* since they have similar leaf blades. Living material of the latter is easily separated in having petioles with the free portion terete or obtusely and weakly sulcate (vs. sharply C-shaped and sulcate in *D. oerstedii*), the base solid green, and in having the sheath decurrent at the apex with one margin overlapping the other (vs. rolled in from both sides in *D. oerstedii*, with both sides visible and often protruded at apex and the sides inequilaterally rounded to auriculate). Compared with *D. oerstedii*, *D. wendlandii* is typically a larger plant with longer stems, thicker internodes, and larger leaves up to 33 cm long and 9.5–15 cm wide, and with the midrib 1.2–1.4 cm wide (vs. 5–6 mm wide for *D. oerstedii*). In addition, *D. wendlandii* has the stigma bowl-shaped at anthesis with a protruded central dome. In contrast, the stigma of *D. oerstedii* is cushion-shaped.

Dieffenbachia oerstedii is similar to *D. killipii* in general blade shape and size as well as in often having the "flat-raised" upper midrib, but *D. killipii*

often differs in having petioles not at all whitish at the base, blades which are typically semiglossy (vs. matte and subvelvety to weakly glossy in *D. oerstedii*), and especially in having the spadix with the pistillate and staminate portions nearly contiguous rather than well separated.

Herbarium material of *Dieffenbachia oerstedii* may be confused with *D. seguine* from the West Indies. Both species sometimes have blades of similar shape, and both have petioles that are comparably sheathed and sharply C-shaped on the free portion. The two species differ in stature, with *D. oerstedii* being much smaller and with blades matte, often subvelvety, whereas those of *D. seguine* are at a minimum weakly glossy on the upper surface. The auricles on the free-ending sheath of *D. seguine* are both rounded at the apex, whereas in *D. oerstedii* one of the sides of the sheath is almost rounded at apex and the other is usually acute at apex. However, the sheaths that subtend inflorescences in *D. oerstedii* may have the apex auriculate on both sides.

The type locality of *Dieffenbachia oerstedii* collected by Oersted remains in doubt but it may be from Guatemala. The type specimen contains only the name "Sanguinillo" on the label. Also penciled on the label is the name "Aguacato," perhaps added at a later date. Engler (1915: 15) cited a collection made by Oersted from "Schottige Berwälder des Berges Aguacate" (perhaps Cerro Aguacate in Sierra de las Minas). He also listed "sanquinello" (Engler, 1915: 15) as a common name for *D. oerstedii* (note the difference in spelling from that original label).

It is possible that *Dieffenbachia oerstedii* occurs in the Lesser Antilles and in French Guiana. *Howard 11744*, purportedly collected along the road between Rousseau and Sulfur Spring on Dominica, appears to be this species. Another specimen collected in French Guiana (*Croat 74319*) along the Cayenne–Regina highway, as well as cultivated material going by the name "*D. oerstedii variegata*" (*Lyon 67-1086*), appears to also represent this species. The same taxon is in cultivation in Port-au-Prince, Martinique (perhaps originating from French Guiana). Since the species is not apparently widespread in the areas mentioned, the field-collected plants may in fact be plants escaped from cultivation. Living specimens studied of the material from French Guiana and the cultivated material from the Lyon Arboretum are characterized by having the midrib creamy white from the lower ¼ to the upper ¼ of the blade. A similar feature is found in some populations of *D. oerstedii* in Costa Rica.

Additional specimens seen. BELIZE. El Dorado, *Schipp 386* (F, GH, K, MO, NY); Caves Branch, halfway up St. Herman's Hill, *Whitefoord 1176* (BM, MO); Cayo, Stann Creek Districts, Hummingbird Hwy., betw. mi. 25–34, *Dwyer & Dieckman 13008* (MO); Vaca Plateau, Vaca Falls, *Balick et al. 2080* (MO); Stann Creek, Cockscomb Basin, Jaguar Pres., 10 km W of Maya Center, off S Hwy., *Balick et al. 2716* (MO); Toledo, vic. of trail to Esperanza beginning 1 mi. N of Columbia Forest Station, *Vanderveen 590* (MO); Columbia For. Stat., *Dwyer 9920* (MO); San José trail to Esperanza 1 mi. N of Columbia Forest Station, *Croat 24250* (MO); San José, 6.7 mi. N of Columbia Forest Station, *Dwyer 11184* (F); Bladen, Richardson Creek, affluent of Bladen Branch, lower part of Maya Mountains, *Davidse & Brant 31879* (MO); along Bladen Branch from Richardson Creek to Quebrada de Oro, *Davidse & Brant 32366* (MEXU, MO); Bladen, Solomon Camp, vic. of the jct. of Richardson Creek and Bladen Branch, foothills of the Maya Mountains, *Davidse & Brant 32410* (MEXU, MO); Bladen, Bladen Nature Reserve, ca. 2 air km N of upper Bladen Branch, *Davidse 35802* (BRH, MO, SEL); Bladen Res., Ek Xux archaeological site, *Davidse & Holst 36041* (MO, MY); upper Bladen Branch basin, along main Bladen Canyon, *Davidse & Holland 36505* (BRH, MO); Columbia Res. near Crique Negro, *Whitefoord 3284* (BR, MO). COSTA RICA. **Alajuela:** Laguna Hule, NE of Cerro Congo, *Luteyn 3342* (DUKE), *Schubert & Rogerson 619* (A); canyon of Río Cariblanco and W slope and summit of ridge between Río Cariblanco and Quebrada Quicuyal, SW of Cariblanco, *Grayum et al. 6194* (MO); 3 km N of La Luisa and 15 km N of Grecia, *Murphy & Jacobs 1289* (DUKE, MO); San Carlos, *Haber & Hammel 1799* (MO); Cordillera de Tilarán, San Ramón-Bajo Rodríguez, vic. La Balsa, 8.9 mi. NW of center of San Ramón, *Croat 68069* (CR, K, MO); 10 km N of Bijagua, *Croat 36473* (DUKE, F, INB, MO); Upala, Brasilia 1.5 km S of town, Finca de Mario Jirón, *Herrera 1636* (INB, MO); 22 km NE of Quesada by air, 4 km W of Muelle San Carlos, *Liesner 14102* (MO); 22 km NE of Quesada by air, 4 km W of Muelle San Carlos, *Liesner 14155* (B, K, MO); 2 km N of Santa Rosa, *Liesner et al 15035* (B, MEXU, MO); Cantón de Upala, Colonia Blanca, Finca Río Negro, *Rivera 1560* (INB, MO); rd. to Los Angeles, NW of church in San Ramón, *Stone 3317* (DUKE); San Ramón-Bajo Rodríguez, 12 km NW of Los Angelos, 16 km NW of San Ramón, *Croat 78830* (MO); vic. km markers 11–12, ca. 7 km NW of Los Angelos, 11–12 km NW of San Ramón, *Croat 78859* (INB, MO); Río Grande de Tárcoles, vic. Capulin, *Standley 40223* (US); Río Segundo, ca. 1 km N of Intl. Airport, *Croat 36855* (MO); Río Zapote, E slopes of Volcán Miravalles, W of Bijagua, *Burger et al. 11695* (F, MEXU, MO); San Carlos (Pital), 1 km N de La Legua, *Hammel 20231* (INB); Río Samen hacia Upala, *Aguilar 5204* (INB, MO); San Ramón, ca. 13 km NW of San Ramón, *Luteyn 3263* (DUKE); along rd. from San Ramón, N of Balsa, ca. 13.8 km N of bridge over Quebrada Volio, *Stevens 13761* (MO); 3.5–4 mi. W of San Ramón, *Croat 46785* (INB, MO); Río Grande, San Isidro, *Carvajal 273* (K, MO); Upala, 13.8 km N of Bijagua, *Croat 36444* (MO); Upala Cantón, Est. Biol. San Ramón, Dos Rios, *Chinchilla 137* (INB, MO); Upala, Río Zapote, 4 km NNE of Bijagua, *Croat 36297* (MO); 3.5 km W of Fortuna, 2.5 km NW of New Volcán Arenal, *Taylor & Taylor 11660* (MO). **Cartago:** slopes of Miravalles above Bijagua, *L. Gómez 19038* (MO); Cantón de Turrialba, 6 km W of La Suiza on the rd. to Pacayitas, *Kennedy & Solomon 4629* (F, INB, MO). **Guanacaste:** SW slopes of Volcán Rincón de la Vieja and Volcán Santa

María, *Burger & Pohl 7825* (F); La Tejona, N of Tilarán, *Standley & Valerío 46000* (US); PN Guanacaste Est. Mengo, Volcán Cacao, *INBio 186* (INB, MO); Tilarán, San Pedro de Río Chiquito, Monteverde, *Haber & Bello 7191* (CR, MO); La Cruz-Santa Cecilia, Finca La Pazmompa, *Ríos et al 109* (CR); PN Rincón, *Rivera 623* (K, MO); Las Nubes de Río Chiquito 1 km NW of village on Cont. Divide, *Haber & Atwood 9163* (INB, MO); PN Guanacaste, Est. Cacao, *Carballo et al. 47* (MO); Cord. de Guanacaste, Rincón de la Vieja, near refugee camp, along rd. NW of Quebrada Grande, *Barringer et al. 4061* (F, MO); PN Guanacaste, Est. Mengo, Volcán Cacao, *INBio 1 186* (CR); Liberia, siguiendo el camino entre Nueva Zelandia (Quebrada Grande) y Dos Ríos, Upala, San Gabriel, *G. Herrera et al. 2928* (MO); Liberia, PN Rincón de la Vieja, Cordillera de Guanacaste, sendero al Volcán, *Taylor 216* (CAS, CR, INB, MO); Nandayure, Península de Nicoya, Bejuco, finca de Abel Rodríguez, *A. Rodríguez & Estrada 142* (CR, INB, MO); Tilarán, *Standley & Valerio 45008* (US); Z.P. Tenorio, Cordillera de Tilarán, Tierras Morenas, Río San Lorenzo, *G. Rodríguez 32* (CR, INB). **Heredia:** Finca La Selva, OTS Field Station on Río Puerto Viejo just E of its jct. with Río Sarapiquí, *Jacobs 2159* (DUKE), *Wilbur 37337* (DUKE), *Wilbur 37243* (DUKE), *Wilbur & Jacobs 34962* (DUKE), *Folsom 8712* (DUKE), *Hammel 8415* (DUKE), *MacDougal 1090* (DUKE), *Wilbur 28249* (DUKE); area between Río Peje and Río Sardinalito, Atl. slope of Volcán Barva, *Grayum 6918* (MO); betw. Río Peje and Río Sardinalito, Atl. slope of Volcán Barva, *Grayum 6925* (MO); PN Braulio Carrillo, betw. Río Peje and headwaters of Río Sardinal, Atl. slope of Volcán Barva, *Grayum & G. Herrera 7829* (CR, MO); 8 km E of San Ramón, *Loiselle 119* (MO); La Selva or Zona Protectora, *Croat 77283* (F, HUA, K, MEXU, MICH, MO, R), *Opler 246* (F); Tirimbina, *Proctor 32251* (LL); San Isidro, Valle Central, below bridge over Rio Tibás, *Valerio 246* (CR). **Puntarenas:** Palmar Norte-Panam border, 3 km N of turnoff to Rincón, *Croat & D. Hannon 79199* (INB, MO, US); ca. 17 km N of San Vito on rd. to Potrero Grande, *Davidson 7164* (MO, RSA); betw. guard station & Quebrada Bonita, Carara Res., *Grayum & Warner 5710* (MO); Ref. Nac. Golfito, along S tributary of Río Cañaza, upstream from crossing of Golfito-Villa Briceño rd., *Grayum 9251* (MO); Jardín Botánico Wilson, W of Río Jaba, 1.5–2 km SW of Las Cruces de Coto Brus, *Grayum 9277* (CR, MO); Finca Loma Linda 1 mi. SW of Cañas Gordas, *Croat 22252* (MO); Quebrada Bonita, to ca. 1 km E of Costanera hwy., Carara Res., *Grayum 4765* (MO); along short rd. to Golfito from Villa Briceño on Inter-am. Hwy., W side of Fila Gamba, ca. 6 km from Golfito airport, *Croat & Grayum 59929* (CR, MO, US); 9 km W of Monteverde on rd. to Inter-Am. Hwy., *Haber & Zuchowski 9251* (F, INB, MO); PN Corcovado Sirena, Monkey Wood, *Kernan 381* (CR, MO); Monteverde, Río San Luis river valley below community on Pac. slope, *Haber et al. 4979* (MO); San Luis, Monteverde Finca de Chepe Rojas, *Bello et al. 42* (CR, G, MBM, MO); 8 km N of Baranca, 1 km N of MiraMar turnoff, W side of km 123 on the Inter-Am. Hwy., Quebrada Negros, *Liesner et al. 15122* (CR, MO); foothills of the Cordillera de Talamanca, vic. of Helechales, along the Río Guineal, *Davidse & Herrera 26262* (CR, MO); Pan-Am. Hwy. km 122, *Hammel et al. 13962* (CR, MO, US); Cantón de Osa, Rancho Quemado, *Quesada 175* (CR, MO, R, UB, VEN); hills N of Palmar Norte, along trail to Jalisco, *Croat 35206* (MO); Est. Quebrada Bonita, Res. Carara, *Croat 79072* (CAS, INB, MO); Orotina-Jaco, in valley of Río Grande Tárcoles, 1 km S of Quebrada Ganado, woods behind Hotel Pink Paradise, near sea level, 5 km S of bridge over Río Agujas on rd. to Jaco, *Croat 79075* (INB, MO); Sector Esquinas, vic. Fila Gamba hills behind Esquinas Rain Forest Lodge, along Quebrada Negra, at end of side rd. off of Villa Bricena to Golfito Rd., *Croat & D. Hannon 79284* (CAS, CM, COL, F, MEXU, MO, NY, SEL, TEX, VEN, WU); Nicoya Peninsula, Curú, *Sanders et al. 19322* (MO); Cantón de Buenos Aires, Ujarrás, headwaters of Río Kuiyé, trail to Olán, *Chacón 364* (F, MO); Coto Brus, Osa Peninsula, Sabanillas de Limoncito, *L. Gómez 22016* (CR, MO); Golfito, Albergue Cerro de Oro, en el Sendero La Tarde, *Moraga 173* (CR, INB, MO); PN Corcovado, Est. Sirena, Sendero Ollas, *Picado & Gamboa 134* (INB, MO); Quebrada Negra, *Marten 831* (F), *Aguilar 2412* (CR, INB, MO, NY); Fila Costeña, Fila Cruces, headwaters of Río Piedras Blancas, Cerro Anguciana, *Grayum et al. 10578* (CR, INB, MO); Est. San Pedrillo, *Aguilar 2380* (INB, MO); Río Sandalo, *Dodge & Goerger 10157* (F); Cordillera de Tilarán, Finca Buen Amigo (Arco Iris), Monteverde, *Fuentes 367* (CR, INB, MO); Finca el Gaucho, *Ocampo 3411* (CR); Península de Nicoya, Est. San Miguel, ca. 2 km S de Malpais, *Hammel et al. 20114* (MO); Granadilla Curridabat, *Valerio s.n.* (ENCB). **San José:** Río Chirripó del Pacífico, General Valley, *Burger & Liesner 7111* (F, MO, PMA); Río Hondura, *Lent 2789* (F); Montañas Jamaica, ca. 3 km NE of Bijagual de Turrubares, Carara Res., *Grayum et al. 5862* (MO); Zona Protectora La Cangreja Forests along Río Negro, ca. 1.5 km E of Santa Rosa de Puriscal, *Grayum et al. 8345* (MO); Quebrada Micos, ca. 8.5 km W of Ciudad Colón, *Grayum & Sleeper 6100* (MO); San José, *Valerio 1355* (F); Bijagua, *L. Gómez 20562A* (MO); Río María Aguilar, *Standley 38942* (US); Mora, Colón, Finca El Rodeo, *Nilsson & Manfredi 505* (F, K); Puriscal, Z. P. La Cangreja, Cerros de Puriscal, Falda W Cerro Cangreja, Santa Gertrudis, Cabeceras Río Negro, *Morales et al. 5413* (INB, MO); Vazquez de Coronado, Braulio Carrillo NP, along Hwy. San José to Siquirres, *Croat 78784* (INB, MO, NY, WU). EL SALVADOR. **Ahuachapán:** *Villacorta et al. 408* (CM, MO); 1–3 mi. above intersection with rd. to Río Cara Sucia, *Croat 42133* (CHIP, MEXU, MO); Finca Colima, Sierra de Apaneca, *Standley 20085* (US); El Imposible, San Benito al N of del Nacimiento del Río Aguachapio, *Sandoval & Chinchilla 352* (MO); La Libertad, *Villacorta et al. 314* (LAGU, MO, US); Finca Los Naranjos, SW of Santa Tecla, *Carlson 153* (F); San Vicente, vic. Ixtepeque, *Standley 21414* (US). GUATEMALA. **Alta Verapaz:** Sierra de las Minas, Quebrada Mercedes, Finca Mercedes, Telemán, Panzós, *E. Martínez et al. 22713* (MEXU, MO); Finca Mercedes, Teleman, Panzós, *E. Martínez et al. 23474* (MO); Río Icvolay, N & NW of Finca Cubilguitz to Quebrada Diablo, *Steyermark 44754* (F); Chimaltenango, Volcán Fuego, above Finca Montevideo, along Barranco Espinazo and tributary of Río Pantaleón, *Steyermark 52070* (F, MO). **Chiquimula:** Municipio Olopa, vic. Olopa, *J. Kufer 391* (M). **Escuintla:** Torolá, *J. D. Smith 2239* (GH, K, NY, US); La Trinidad, *Standley 65041* (F); between Río Jute and Río Pantaleón, *Standley 63529* (F), *Standley 63620* (F); Torolá, *D. Smith 7813* (MO). **Guatemala:** Finca la Aurora, *Aguilar 256* (F). **Huehuetenango:** Sierra de los Cuchumatanes, *Steyermark 49321* (F). **Izabal:** above Selempim along rd. to Bocancha and base of Sierra de Las Minas, *Förther 10213* (M); Montaña del Mico, *Steyermark 38775* (F); near Quiriguá, *Standley 72447* (F); ca. 1 mi. E of Santo Tomas, *Croat 41855* (GUAT, MO); Selempim-Bocancha, base of Sierra de Las Minas, *Förther et al. 10213 {232}* (MO, MSB); Montana del Mico, *Steyermark*

38647 (F). **Jutiapa:** vic. Jutiapa, *Standley 75669* (F); between Mita and Asunción Mita, *Steyermark 31763* (F). **Petén:** between Finca Yalpemech on Río San Diego and San Diego on Río Cancuen, *Steyermark 45410* (F). **Quezaltenango:** Retalhuleu, near Chivolandia along rd. to San Felipe, *Standley 87180* (F). **Retalhuleu:** Pueblo Nuevo, *Stricker 342* (US); Río Samalá, vic. San Felipe, *Steyermark 34555* (F). **Sacatepéquez:** below Barranco Hondo, *Standley 88988* (F). **San Marcos:** 3 km SW of San Rafael Pie de Cuesta, *Harmon & Fuentes 4740* (MO); Río Chopal, Finca El Porvenir, S-facing slopes of Volcán Tajumulco, *Steyermark 37456* (F); Volcán Tajumulco, *Steyermark 37153* (F); near El Molino, *Standley 78523* (F); Río de los Esclavos valley, near El Molina, *Standley 60715* (F); Volcán Tecuamburro, *Heyde & Lux 4654* (GH, K, NY, US). **Sololá:** S-facing slopes of Volcán Atitlán, above Finca Mocá, *Steyermark 47908* (F). **Suchitepéquez:** near Pueblo Nuevo, *Standley 66844* (F); near Las Lajas, *Standley 58291* (F). HONDURAS. Coyol, *Carleton 508* (US), *Standley 26305* (F, GH, US). **Atlántida:** along rd. for municipal water supply of Tela, Lancetilla Botanical Gardens, on rd. ca. 2 mi. WSW of Tela and S of main hwy., *Croat & D. Hannon 64622* (MO, TEFH, US); Campamento Quebrada Grande ca. 10 km SW of La Ceiba, base of N slope of Pico Bonito, *Liesner & Mejía 26236* (MO); Lancetilla, 4 km S of Tela, *Mena 190* (TEFH); sendero a la Pica, El Dorado, *Cruz 354* (TEFH); ca. 3 mi. S of Tela, *Webster et al. 12624* (US), *Webster et al. 12625* (F, MO, US); Tela, valley above Exp. Stat., *MacDougal et al. 3193* (ENCB, F, MO, NY), *MacDougal et al. 3299* (MO); near Tela, *Pfeifer 2163* (US), *Standley 52702* (F, US); 10 mi. SE of Tela along Río Lancetilla, *Croat 42645* (INB, MEXU, MO, PMA, TEFH); Río San Alejo, S of San Alejo, *Standley 7700* (F), La Ceiba area, 35 km S of La Ceiba on rd. to Olanchito, *Madison 712* (GH); La Ceiba, Mt. Cangrejal, Mt. Cangrejal, La Ceiba area, *Yuncker et al. 8395* (F, GH, K, MO, US). **Comayagua:** ca. 2 km S of Lake Yojoa, *Balick et al. 1738* (MO). **Copán:** 24 km E of Santa Rita, *Harmon & Dwyer 4035* (MO, MEXU); Nueva Arcadia, 6 mi. S, *Harmon & Fuentes 6419* (MO). **Gracias a Dios:** Ahuas Bila, 200 km SW of Puerto Lempira, *Nelson & Cruz 9215* (MO, TEFH, UMO). **Yoro:** Cordillera Nombre de Dios, hills S of San Jose de Texiguat, *Davidse et al. 34478* (MO). MEXICO. **Campeche:** El Maculisal, 40 km al sur de la carretera, Escarciga, Chetumal, *Bravo s.n. (MEXU 30199)* (MEXU). **Chiapas:** Chiapas, *Cabrera et al. 1937* (MO); Izabal, Mpio. Livingston, *E. Martínez et al. 23175* (MEXU); 2 mi. S of Chiapas border along Hwy. 195, 8 mi. N of Pichucalco, *Croat 40087* (MO), *Croat 40089* (MO); 60 mi. SE of Palenque, *Croat 40163* (CHIP, MO); near ruins at Palenque, *Spellman et al. 164* (F, MO, NY); 2.5 mi. N of Isthuatan, *Croat 47868* (MO); Bochil-Pichucalco, 17.1 km SW of Pichucalco, *Croat 78678* (MO); 20 km S of Palenque on rd. to Ocosingo, *Mayo & Madison 301* (K); Mpio. Ixhuatán, *Clarke 60* (DS); Ococingo, 19 km NW of Crucero Corozal, *E. Martínez 13445* (MEXU, MO); Tenejapa, along Río Tanate at Habenal, paraje of Mahbenchauk, *Breedlove 12752* (F); Palenque Archaeological Site, 3 mi. S of Palenque, *Thorne & Lathrop 40559* (RSA); Río Cuxtepeques, near Finca Gadow, *Breedlove 40155* (DS); Las Margaritas, *Breedlove & McClintock 34192* (DS); Mapastepec, Río Testecapa, 10 km SE of Mapastepec, *Breedlove & Thorne 30681* (DS); Ocosingo, 5 km SW of Santo Domingo, 120 km SE of Palenque on rd. to Bonampak, *Davidse et al. 20440* (CM, MEXU, MO); Ocosingo, 3 km NW of Vertice del Chixoy camino a Boca Lacantum, *E. Martínez S. 13630* (MEXU); Río Usumacinta, at ruins of Yaxchilán, *Breedlove 33839* (DS); vic. Palenque archaeological site, *Davidse et al. 20326* (MEXU, MO); 6–12 km S of Palenque on rd. to Ocosingo, *Breedlove 34977* (DS); Pichucalco, cerca Campo Aviacion, *F. Miranda 7546* (MEXU); Solusuchiapa, 2–4 km below Ixhuatan along road to Pichucalco, *Breedlove 24166* (DS). **Oaxaca:** Choapan, Mpio., San Juan Lalana, trail Jalahui–Arroyo San Pedro, *Noriega & H. Vasquez G. 1353a* (MEXU). **Tabasco:** Cerro las Campanas, 3 km E of Teapa, ca. 50 km S of Villahermosa, *Conrad et al. 2863* (MO); vic. of Teapa, Teapa-Tacotalpa, 3.1 m E of Teapa, *Croat & D. Hannon 65370* (MEXU, MO); 3 km E of Teapa along rd. to Jalapa, *Croat 40107* (MO); Grutas de Ocona near Teapa, *Davidse et al. 29516* (MEXU, MO); Tacotalpa, 3 km E of Lázaro Cárdenas, *Cowan 2063* (MEXU, MO); Teapa, Cerro las Campanas, 3 km E of Teapa, ca. 50 km S of Villahermosa, *Conrad & Conrad 2882* (MO). **Veracruz:** Cordova, *Bourgeau s.n.* (P); Las Palmas-Catemaco, km 18, *Leija & Garza 3341* (MEXU); Las Palmas-Catemaco, km 18, C-12-A, *González 3341* (MEXU); Las Cruces, Las Choapas, *Gómez-Pompa 1505* (F); Ebiotrolotu, *Anaya 1* (MEXU); 6.5 km from Santiago Tuxtla and 3.6 km on trail to Cerro del Vigía, *González 5597* (MEXU); Catemaco, 10 km N of Sontecomapan, vic. Hotel Playa Escondida, *Nee 23733* (B, F, GH, MEXU, MO, NY); E side of entrance of Laguna de Sontecomapan into the Gulf of Mexico, 7 km NE of Sontecomapan, *Nee 22595* (F, MO); Cerro Cochinitos, near Catemaco, *R. Hernández 542* (F, MEXU, US); Playa Escondida, 12 mi. airline NNW of Sontecomapan, *Holstein & Armbruster 20425* (UC); ca. 8 mi. S of Catemaco near Zapoapan on rd. to Acayucan, *Moore Jr. & Bunting 8928* (BH); 5.7–6 mi. from Catemaco on rd. to Santecomapan, *Moore Jr. & Bunting 8933* (BH); Catemaco-Montepio, 12.1 km beyond end of asphalt hwy. portion, 22.2 km N of Catemaco, along border trail to the Los Tuxtlas Res., *Croat 78687* (MO); along rd. between Catemaco and Montepio, 2.6 km S of Los Tuxtlas Field Station, *Croat 78695* (MO, WU); 3 mi. SW of Sontecomapan, Los Tuxtlas, *Barlow s.n.* (US); Chinameca, Pajapan, *Tellez et al. 4466* (MEXU); Coatzacoalcos, 6 mi. E of Coatzacoalcos, Hwy. 180, *Croat 40062* (CM, MO, QCA, TEFH); Hidalgotitlan, 3 km SW of Campamento La Laguna, *Nee 29993* (F, M, NY, XAL); Hidalgotitlan, 1 km SE of Agustín Melgar, *Nee 29752* (MO); Río Soloxuchil, entre Hnos. Cedillo y la Escuadra, *M. Vasquez et al. V-907* (XALU); Las Choapas, Las Cruces, *Nevling & Gómez-Pampa 1505* (F); Misantla, 8 km S of Misantla on rd. to Xalapa, *Madison 589* (GH, SEL); San Andres Tuxtla, Est. de Biol. Tropical Los Tuxtlas, N of San Andrés Tuxtla between Sontecomapan and Montepio, *Croat & D. Hannon 63129* (MEXU, MO), 19 Aug. 1972, *Madison 627* (GH); San Andres Tuxtla, N and E sides of Laguna Encanatada, 3 km NE of San Andres, *Nee et al. 24759* (F, K, MO, NY, SP, XAL), *Ibarra 455* (MEXU), *Ibarra & Cedillo 1804* (MEX, MO, NY), *Ibarra 645* (MEXU, MO), *Dillon et al. 1837* (F, MO, NY), *Cedillo T. 3645* (MEXU, MO), *Calzada 338* (F, MEXU), *Chazaro 416* (F, MEXU); Monte Pío, 15 km al W de Catemaco, *L. González 1473* (ENCB, MEXU); Santiago Tuxtla, 6.5 km de Santiago Tuxtla y 3.6 km camino al cerro del vigia, *Leija & Garza 5597* (MEXU); Santiago Tuxtla, cerca Madero, *Ramamoorthy et al. 3763* (MEXU); Tezonapa, 5 km SW of Motzorongo, vic. Felipe E. Martínez, *R. Robles G. 815* (MEXU, XAL); Tlapacoyan, along Río Tablazos, upstream from Puente de Tomata, 6 km SSW of Tlapacoyan, *Nee et al. 26103* (F, NY, XAL). PANAMA. **Chiriquí:** vic. David, *Pittier 2836* (MO); 13–20 km W of Río Chiriquí Viejo, *D'Arcy 10766* (MO); rd. to Río Serrano, *Folsom et al. 2111*

Figure 21. *Dieffenbachia panamensis.* —A. Habit of flowering plant (*Croat 67526*). —B. Potted plant showing ovate blades (*Cirino s.n.*). —C. Habit showing ovate-elliptic blades and inflorescences (*Croat 74856*). —D. Crown of plant with blade showing quilted blades and close-up of open inflorescence (*Croat 67526*).

(MO); W of Tolé, Río Cuvibora, *Hammel 6264* (MO); Burica Peninsula, vic. of Puerto Armuelles, San Bartolo Limite, 10–12 km W of Puerto Armuelles, *Croat 22173* (MO). **Coclé:** 4–6 km N of El Copé, *Montenegro & Chung 1462* (PMA, STRI), *Aranda et al. 2860* (PMA); La Mesa, N of El Valle de Antón, 2 km W of Cerro Pilón, *Croat 37351* (MO). **Veraguas:** vic. Santa Fé, 1.7 km past Escuela Alto Piedra, *Croat & Zhu 76859* (MO); 6–7 km past school, *Nee 99121* (MO), *Luteyn & Wilbur 4569* (DUKE).

Cultivated plants. Mexico. Veracruz: Catemaco, cultivated, *Bunting 1692*, Lankester Gardens, Cultivated, *Kew 70-76-494* (K); Finca La Selva, originally collected by Helen Young, 17 June 1971, *Croat 68449* (CM, CR, MO).

21. Dieffenbachia panamensis Croat, sp. nov. TYPE: Panama. Coclé: vic. of El Copé, 4.1 mi. N of village, along old logging road which leads down to the lowlands, 8°39′N, 80°36′W, 680–770 m, 25 Mar. 1993, *T. B. Croat 74856* (holotype, MO-4342614!; isotypes, B!, CAS!, COL!, DUKE!, F!, GH!, INB!, L!, K!, MEXU!, NY!, PMA!, UB!, US!, VEN!). Figures 21, 30A.

Planta 0.75–2.5 m; internodia brevia, 3–4 cm diam.; petiolus 10–14 cm longus, vaginatus ad apicem; vagina effusa; lamina ovata ad elliptica, (26)45–75 cm longa, (13.5)17–40 cm lata; inflorescentia 3 per axillam; pedunculus 10–18 cm longus; spatha 13–20 cm longa; spadix 12–18 cm longa, cum parte pistillata 5–9 cm longa.

Stout erect herb, 0.75–2.5 m tall; *internodes* short, typically more than twice as broad as long, 1–3 cm long (typically somewhat longer on one side than on the other), 3–4(5) cm diam., dark green,

moderately glossy. LEAVES rosulate, erect-spreading to spreading; *petioles* (6)10–14 cm long (averaging 10.6 cm long), moderately erect, dark green (white at base), sheathed throughout, the margins flaring to recurled, sometimes incurled, markedly crisped-undulate nearly throughout; *blades* ovate to elliptic, (26)45–75 cm long, (13.5)17–40 cm wide (averaging 45.9 × 24.4 cm), 1–2.4 times longer than wide (averaging 1.6 times longer than wide), markedly inequilateral (one side 2.5–5 cm wider than the other), obtuse to rounded at apex (the tip inequilateral and weakly acute to acuminate), acute to rounded at base, moderately coriaceous, moderately bicolorous, dark green, matte and somewhat velvety to glisteningly velvety above, weakly quilted and minutely wrinkled on upper surface, much paler to moderately paler and slightly glossy to matte below, drying dark blackish brown to dark yellowish brown above, yellowish brown to grayish brown below; *midrib* broadly convex or sometimes flattened, 1.5–2 cm wide, slightly paler above, somewhat more convex and slightly paler below; *primary lateral veins* moderately quilted, (7)10 to 20 per side, arising at an acute angle, then spreading at 45°–60° angle, often at a somewhat wider angle on one side, obtusely sunken above, convex to obscurely raised and darker below; interprimary veins usually 1 per pair of primary lateral veins, about equal to primaries; minor veins not visible. INFLORESCENCES 3 per axil; *peduncles* 10–18 cm long (averaging 12.5 cm long), somewhat flattened, medium green, matte, weakly striate drying, to 6–10 mm diam.; *spathe* 13–20 cm long (averaging 18.4 cm long), medium to pale green, weakly and finely striate on back surface, with darker, oblique lines extending out to the margins, inner surface slightly paler; *spadix* 12–18 cm long; free part 8.5 cm long; pistillate portion 5–9 × 1.8–2.2 cm, narrowed slightly toward the apex; sterile staminate portion 3–4.2 × 1–1.2 cm; mostly sterile intermediate section 1.2 cm long, with a few scattered staminodia in the lower half; fertile staminate portion 5–7 cm long, the flowers irregularly 5-sided, 2.5–3 mm diam.; pistils 3.5–4 mm diam., irregularly rounded at apex, closely packed, almost contiguous; staminodia club-shaped, 4–5 mm long, generally extending above the pistils, broadest at base and apex, the tips 1.5–2 mm diam. Fruits orange.

Distribution and habitat. *Dieffenbachia panamensis* ranges principally along the Atlantic coast of Panama from 50 to 850 m, on both slopes along the Continental Divide east of the Canal Area.

Phenology. There are not enough collections of this species to be certain of its flowering and fruiting phenology. However, flowering collections have been made in January, March, July, and September, and fruiting collections during September and November.

Discussion. The species is recognized by its fully sheathed petioles that are usually flaring to recurled, by the moderately coriaceous, somewhat velvety, weakly quilted blades, and usually broadly convex midribs. It has up to three large inflorescences (mostly more than 30 cm long) per axil.

The species may be most closely related to *D. standleyi*, which ranges from Nicaragua to Honduras along the Atlantic slope. Both share petioles mostly fully sheathed, and have the sheath margins rolled outward, but *D. panamensis* differs in having blades more coriaceous, matte, and somewhat velvety to glisteningly velvety above, weakly quilted and minutely wrinkled on the upper surface.

Though the species does not occur in the same area, it could be confused with *D. horichii*, a species with a similarly fully sheathed petiole, but the margins of which are incurled rather than flaring. The blades of *D. horichii* dry mostly greenish rather than somewhat blackened. *Dieffenbachia horichii* is restricted to the Pacific slope of Costa Rica, ranging from sea level to 900 m, while *D. panamensis* is primarily known from the Atlantic slope of Panama (also known from the Pacific slope at higher elevations).

Paratypes. PANAMA. **Coclé:** Alto Calvario, 7 km N of Copé, *Folsom et al. 8264* (MO); Alto Calvario, old lumber trail to Las Ricas, Limón & San Juan, *Croat 68820* (MO); Alto Calvario Region, 4.5 mi. N of El Copé, 2.5 mi. N of Escuela Barrigón, *Croat 67526* (MO); 8 km above El Copé, *Hammel 778* (MO), *Folsom & Collins 6486* (MO). **Darién:** Río Tuquesa, ca. 2 air km from Cont. Div., vic. of Kittredge gold mine, *Croat 27206* (MO). **Panamá:** above El Copé, 28 km NW of Penonomé, *Read & Watson 84-75* (US).

22. Dieffenbachia pittieri Engl. & K. Krause, Pflanzenr. IV. 23 Dc(Heft 64): 42. 1915. TYPE: Panama. Canal Area [Colón]: Gamboa-Las Cruces [currently Madden Forest Reserve], 50–80 m, 2 July 1911, *H. F. Pittier 3766* (holotype, US!; isotype, B not seen). Figures 22, 29B.

Herb, to probably less than 1 m tall; internodes 1–1.5 cm long, 1.5–2 cm diam., smooth, drying dark yellow-brown with conspicuous pale petiole scars; *petioles* 10–11 cm long, fully sheathed, free-ending and weakly auriculate on both sides at apex; *blades* obliquely oblong, 17.8–20.5 cm long, 6–8.0 cm wide, 2.9–3.1 times longer than wide, 1.8 times

Figure 22. *Dieffenbachia pittieri*. Herbarium type specimen.

longer than petioles, shortly acute and markedly inequilateral above, acute to obtuse at base; *primary lateral veins* 6 to 7 per side, concentrating mostly in lower half of the blade, extending parallel to the midrib, then spreading at 25°–30° angle, nearly straight to weakly curved to the margin and sweeping up along the margin, drying moderately obscure above, convex and darker than surface below; minor veins parallel with obscure and irregular cross-veining on drying; surface drying matte, moderately dark yellow-brown above, light brown and finely pale-speckled below. INFLORESCENCES 2 per axil; *peduncles* 3.5–5 cm long, drying light brown, 2 mm diam.; *spathe* 17 cm long, to 3.5 cm wide when flattened; spadix 14.5 cm long; pistillate portion of spadix to 8.5 cm long, 4 mm wide; staminate portion of spadix 5 cm long; mostly sterile segment 2.2 cm long, drying 2 mm diam., with a few scattered cup-like pistillodes throughout its length; pistils 59, borne in a cup-like disk; staminodia mostly missing.

Distribution and habitat. *Dieffenbachia pittieri* is known only from the type in the Isthmus of Panama in an area of *Tropical moist forest* (T-mf) life zone (Holdridge, 1967) at less than 200 m elevation. It is most unusual to encounter an endemic species in this life zone, but the species is distinct from other species in *Dieffenbachia*. There is a possibility that this could be a hybrid between *D. killipii* and *D. isthmia* because hybridization does occur in the wild in *Dieffenbachia*. Its greatest resemblance is with *D. killipii*, which also occurs in this area and dries a similar color. *Dieffenbachia pittieri* differs from *D. killipii* in having a dark brown, smooth-drying stem (light yellow-brown, usually conspicuously ridged stems for *D. killipii*), fully sheathed petioles (usually with the petiole sheath ending well below the base of the blade for *D. killipii*), blades with the midrib flat on the upper surface ("square-raised" for *D. killipii*), and a spadix with the pistillate and staminate portions widely separated by a long, mostly sterile portion (vs. with the pistillate and staminate portions more or less contiguous in *D. killipii*).

Dieffenbachia pittieri has been confused with *D. obscurinervia* (Standley, 1944; Croat, 1978), but it proved to share little in common with that species once the type specimen was examined. It differs from that species in having smooth, not scurfy stems, unspotted, fully sheathed petioles, blades with distinct primary lateral veins and with a midrib flat, not "square-raised" above, and a spadix with pistillate and staminate portions separated by a broad sterile segment rather than having them contiguous or nearly so.

23. Dieffenbachia seguine (Jacq.) Schott, Wiener Z. Kunst 1829(3): 803. 1829. *Arum seguine* Jacq., Enum. Syst. Pl. 30. 1760. *Arum seguinum*, orth. var. *Caladium seguinum* (Jacq.) Vent., Mag. Encycl. 30. 1801. *Dieffenbachia plumieri* Schott, Oesterr. Bot. Wochenbl. 69. 1852. TYPE: Plumier, Descr. Pl. Amer. tab. 61 (lectotype, designated here). Figures 23, 30B.

Caladium maculatum Lodd., Bot. Cab. tab. 608. 1822. *Dieffenbachia maculata* (Lodd.) G. Don, in Sweet, Hort. Brit. ed. 3, 632. 1839. *Dieffenbachia maculata* (Lodd.) Bunting, Baileya 10: 145. 1963, nom. superfl. TYPE: Lodd., Bot. Cab. tab. 608. 1822 (lectotype, designated here).

Dieffenbachia literata Schott, Oesterr. Bot. Wochenbl. 68. 1852. *Dieffenbachia seguine* fo. *liturata* (Schott) Engl., Fl. Bras. 3(2): 175. 1878. *Dieffenbachia seguine* subvar. *liturata* (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. *Dieffenbachia seguine* var. *liturata* (Schott) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 47. 1915. TYPE: based on a cultivated collection fide Schott (not seen). Schott painting 1874 serves as the type [microfiche 64. c 7] (lectotype, designated here).

Dieffenbachia lineata K. Koch & Bouché, Index Sem. (Berlin) 14. 1853. *Dieffenbachia seguine* fo. *lineata* (K. Koch & Bouché) Engl., Fl. Bras. 3(2): 175. 1878. *Dieffenbachia seguine* subvar. *lineata* (Schott) Engl., Bot. Jahrb. Syst. 26: 569. 1899. *Dieffenbachia seguine* var. *liturata* (Schott) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 47. 1915. TYPE: New Granada, based on a cultivated collection at the Berlin Botanical Garden, not seen. Schott illustration 1867 serves as the type [microfiche 64 d 7] (lectotype, designated here).

Dieffenbachia robusta Schott, Oesterr. Bot. Wochenbl. 65. 1854. *Dieffenbachia seguine* var. *robusta* (K. Koch) Engl., Bot. Jahrb. Syst. 26: 568. 1899. TYPE: Locality unknown, cultivated collection of unknown origin at Berlin Botanical Garden. Schott illustrations 1907–1908 serve as the type [microfiche 66 b2, b3] (lectotype, designated here).

Dieffenbachia consobrina Schott, Syn. Aroid. 131. 1856. TYPE: Brazil. Rio Negro, *Martius s.n.* (holotype, M!).

Dieffenbachia poeppigii Schott, Syn. Aroid. 130. 1856. TYPE: Peru. Without locality, *Poeppig s.n.* (holotype, W destroyed during World War II); Schott illustration 1903 serves as the type (microfiche 64. b 6) (lectotype, designated here).

Dieffenbachia cognata Schott, Syn. Aroid. 130. 1856. TYPE: Suriname. Paramaibo, *Martius s.n.* (holotype, M). [See also Schott paintings 1845 & 1846.]

Dieffenbachia gollmeriana Schott, Oesterr. Bot. Z. 8: 387. 1858. TYPE: Venezuela. Without locality, *Gollmer s.n.* (holotype, B apparently lost); Schott drawing 1857 (microfiche 64 b. 7) serves as the type (lectotype, designated here).

Dieffenbachia neglecta Schott, Bonplandia 7: 30. 1859. TYPE: Jamaica. Without locality, *Distin* (holotype, K!).

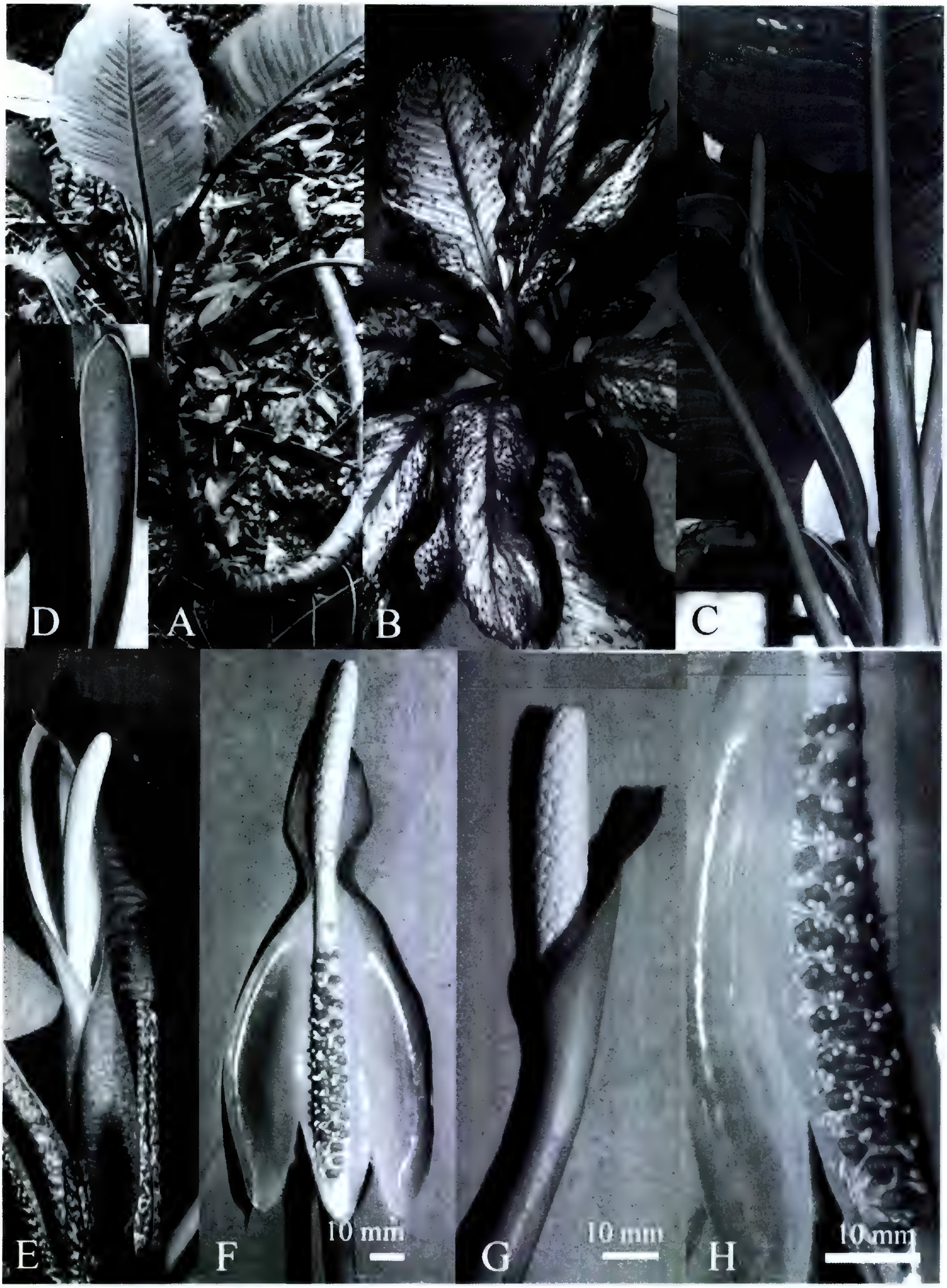


Figure 23. *Dieffenbachia seguine.* —A. Habit of plant showing the long creeping caudex and erect portion of stem apex (*Croat 60613*). —B. Potted plant showing habit and leaves with variegated blades and inflorescences at anthesis (*Croat 69695*). —C. Close-up of crown of plant with abaxial surfaces of blades and side view of the spathe (*Croat 53921*). —D. Petiole showing slightly free-ending, inequilateral sheath and acutely sulcate free portion above sheath (*Croat 68494*). —E. Crown of plant showing speckled petioles and inflorescence at anthesis (*Croat 77298*). —F. Spathe at anthesis, cut open to show inner surface of tube. —G. Close-up of inflorescence showing apical half with spathe blade somewhat spreading and staminate portion of spadix protruding somewhat forward. —H. Portion of spadix showing bicarpellate pistils. F, G, H. (*Croat 71828*).

Dieffenbachia ventenatiana Schott, Bonplandia 7: 30. 1859. *Dieffenbachia seguine* subvar. *ventenatiana* (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. *Dieffenbachia seguine* var. *ventenatiana* (Schott) Engl. Pflanzenr. IV, 23 Dc(Heft 64): 48. 1915. TYPE: Suriname. Without locality, *Hostmann s.n.* (holotype, K!).

Dieffenbachia lingulata Mart. ex Schott, Prod. Syst. Aroid. 334. 1860. *Dieffenbachia seguine* var. *lingulata* (Mart. ex Schott) Engl., Fl. Bras. 3(2): 175. 1878. *Dieffenbachia seguine* subvar. *lingulata* (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. TYPE: Brazil. Pará: *C. Martius 3307* (holotype, M!).

Dieffenbachia irrorata Schott, Prod. Syst. Aroid. 335. 1860. *Dieffenbachia seguine* fo. *irrorata* (Schott) Engl., Fl. Bras. 3(2): 175. 1878. *Deffenbachia seguine* subvar. *irrorata* (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. *Dieffenbachia seguine* subvar. *irrorata* (Schott) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 48. 1915. TYPE: Brazil. Pará: *C. Martius 2640* (holotype, M!).

Dieffenbachia conspurcata Schott, J. Bot. 2: 52. 1864. *Dieffenbachia seguine* fo. *conspurcata* (Schott) Engl., Fl. Bras. 3(2): 175. 1878. TYPE: Brazil. Pará: Schott paintings 1849 & 1850 (microfiche 65 b5 & b6) serve as the type (lectotype, designated here).

Dieffenbachia barraquiniana Verschaff. & Lem., Ill. Hort. 11: t. 387. 1864. *Dieffenbachia seguine* fo. *barraquiniana* (Verschaff. & Lem.) Engl., Fl. Bras. 3(2): 174. 1878. *Dieffenbachia seguine* subvar. *barraquiniana* (Verschaff. & Lem.) Engl., Bot. Jahrb. Syst. 26: 568. 1899. *Dieffenbachia picta* var. *barraquiniana* (Verschaff. & Lem.) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 50. 1915. TYPE: not designated; the illustration in Ill. Hort. 11: t. 387. 1864, serves as the type (lectotype, designated here).

Dieffenbachia gigantea Verschaff., Ill. Hort. 13: t. 470, 471. 1866. *Dieffenbachia picta* subvar. *gigantea* (Verschaff.) Engl., Bot. Jahrb. 26. 569. 1899. TYPE: not designated; the illustration in Ill. Hort. 13: 470–471. 1866, serves as the type (lectotype, designated here).

Dieffenbachia wallisii Linden, Ill. Hort. 17: t. 11. 1870. *Dieffenbachia seguine* subvar. *wallisii* (Linden) Engl., Pflanzenr. IV 23 Dc(Heft 64): 47. 1915. TYPE: Brazil. Rio Negro, 1866, *Wallis s.n.* (holotype, K!).

Dieffenbachia brasiliensis Veitch, Cat. 12. 1875. *Dieffenbachia picta* fo. *brasiliensis* (Veitch) Engl., Fl. Bras. 3(2): 176. 1878. TYPE: Brazil. Not designated; drawing on p. 12 of Veitch Cat. serves as the type (lectotype, designated here).

Dieffenbachia picturata L. Linden & Rodigas, Ill. Hort. 39: 101. t. 163. [CLXII] 1892. *Dieffenbachia picta* Schott subvar. *picturata* Engl., Bot. Jahrb. Syst. 26: 570. 1899. TYPE: Venezuela. Illustration in Ill. Hort. vol. 39: t. 163. 1892, serves as the type (lectotype, designated here).

Dieffenbachia seguine (Jacq.) Schott subvar. *ventenatiana* (Schott) Engl., Bot. Jahrb. Syst. 26: 568. 1899. *Dieffenbachia seguine* (Jacq.) Schott, var. *ventenatiana* (Schott) Engl., Pflanzenr. IV. 23 Dc(Heft 64): 48. 1915. *Dieffenbachia ventenatiana* Schott, Bonplandia 7: 30. 1859. TYPE: Suriname. *Hostman* (K!).

Herb, to 1.5 m tall; stems reclining at base then erect; *internodes* 1.7–5 × 1.5–4.0 cm, medium green and glossy soon becoming dark green, semiglossy to almost matte, smooth. LEAVES arching; *petioles* 10–34.5 cm long, averaging 29.7 cm long, medium green and weakly glossy, rarely white, sometimes densely pale green maculate, sheathed ⅔–⅘ or more their length, free part of petiole 5–7 cm long, acutely sulcate; sheath 20–28 long, pale green and matte on inside, usually acute on one side, rounded on the other side, sometimes inequilaterally acute on both sides, curved inward along the margins but the sides not contacting, faintly striate throughout but especially noticeable toward the base, the basal portion of the sheath often persisting after much of the petiole falls free; *blades* ovate-lanceolate, 17–38.5 cm long, 10–20 cm wide (averaging 32.1 × 17.3 cm), 2.7–3.3 times longer than wide, 1.2–1.6 times longer than petioles, inequilateral, one side 1.5 cm broader, inequilaterally rounded at base or with one side acute the other rounded, subcoriaceous, semiglossy, medium-dark green, sometimes mottled with pale green or white, especially along midrib, moderately paler below; *midrib* flattened-convex and slightly paler, ca. 6 mm wide above, narrowly rounded and slightly paler below, sometimes darker green-maculate in lower half; *primary lateral veins* 13 to 15(19) per side, arising at 40°–50° angle, quilted-sunken and concolorous above, concolorous and concave below; interprimary veins usually present and nearly as conspicuous as primary lateral veins; minor veins moderately indistinct, arising from the midrib and paralleling the primary lateral veins. INFLORESCENCES 1 to 4 per axil, usually solid green but sometimes pale greenish yellow maculate throughout (maculations sometimes appearing in irregular transverse rows on spathe); *peduncles* 2.5–14 cm long, 7–8 × 8–12 mm diam., medium green, weakly glossy, faintly dark green-striate; *spathe* 11–24 cm long, abruptly acuminate at apex, gradually constricted above tube, in the upper ⅔, medium-dark green and semiglossy to matte outside, slightly paler and glossy within; spathe blade at anthesis stiffly erect then recurving near apex; spathe tube 7–10 cm long, 1.2–1.8 × 2.0–2.5 cm diam.; *spadix* 10–19 cm long; the naked portion at base 1.5–2.5 cm long; pistillate portion of spadix 4–8.5 cm long; pistils 20 to 25, closely aggregated except in upper 10–12 mm, with up to 3 of them in a loose spiral across the spadix but usually with 1 or 2 at any level on the spadix; ovary bicarpellate, markedly bilobate, rarely 3- or 4-locular (and 3- to 4-lobate, respectively), pale green, semiglossy, 3.2–3.6 × 2.1–2.4 mm; stigmas pale orange, doubled (one for each locule) but usually fused along the adjoining margins, 2.3–4.3 × 2.0–2.4 mm diam.; staminodia

4 per pistil, 2.8–3.1 mm long, 0.8–1.0 mm wide at apex, slightly thickened toward apex, flattened and free at base, the base equally as wide or up to twice as wide as the apex; fertile staminate portion of spadix 5–7.5 cm long, 5–15 mm diam., slightly broader midway, tapering slightly toward both ends, bluntly acute to rounded at apex, at anthesis protruding forward out of spathe and usually being trapped there by the closing spathe; staminate flowers 5 to 6(8?) per spiral, (1.6)2.2–3.5(4) mm diam., squarely rounded to rounded, sometimes broadest perpendicular to the axis, smoothly rounded at apex, sometimes with a transverse linear slit medially; anthers 5 to 6 per synandrium, shedding their pollen well below the rim of the synandrium; the mostly naked portion of spadix 2.0–4.0 cm long, 6–8 mm diam., medium green with 1 pistil in lower ⅓ and with 2 to 3 staminodes in upper ½, sometimes with only a few staminodia scattered in upper ¾. *Berries* bright red or orange.

Distribution and habitat. *Dieffenbachia seguine* ranges throughout much of the West Indies from Cuba (Ileana Arias, Havana, pers. comm.), Jamaica, Hispaniola, and Puerto Rico, through the Lesser Antilles to Trinidad and South America, there ranging throughout much of Venezuela (Amazonas, Aragua, Apure, Bolívar, Carabobo, Delta Amacuro, Distrito Federal, Falcón, Lara, Miranda, Monagas, Nueva Esparta, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, Zulia), especially in the Cordillera de la Costa, to Guyana and Suriname (Boggen et al., 1992), French Guiana, eastern Brazil (Amapá, Amazonas, Goiás, Maranhão, Pará, Rondônia, São Paulo), and west to the lowlands of Colombia (Meta, Vaupes, Vichada), eastern Ecuador (Napo), and Bolivia (Pando, Santa Cruz).

Dieffenbachia seguine flowers and develops mature fruit to some extent all year-round, but with more flowering occurring in the late dry season and throughout the early part of the dry season between March and September.

The species is characterized by having petioles that are shorter than the blade and sharply sulcate on the free portion, with the sheath margins acute to rounded at the apex and with ovate-lanceolate blades. The best character for separation of the species, however, is the unusual inflorescence with large, bicarpellate ovaries and a spathe that is somewhat spread backward while the staminate portion of the spadix protrudes prominently forward and persists after the spathe has closed.

The species was long considered to be a common species in Central America but that material proved to be mostly *D. oerstedii*, and in some cases, *D. wendlandii*. The latter species was even erroneously synonymized with *D. seguine* by Engler (1915). Both species sometimes have blades of similar shape, and both have petioles that are comparably sheathed and sometimes sharply C-shaped on the free portion. However, *D. wendlandii* differs in having pistils with a single ovule. The staminate spadix of *D. wendlandii* is also more or less tapered toward the apex and not protruding strongly forward at anthesis, whereas in *D. seguine* the spadix is stubby-ellipsoid.

I agree with Bunting (1979), who synonymized both *D. picta* Schott and *D. maculata* (Lodd.) G. Don under *D. seguine*. This species has been the most confusing of all Araceae in the number of epithets (subspecies, varieties, subvarieties, and forms) recognized, over 60 in all. Some are varieties of *D. picta*, others varieties of *D. seguine* or combinations between the same two taxa. It is not clear why this should be so. Throughout its range it is no more variable than any other species of *Dieffenbachia*, but it is quite widespread and this brings it into contact with more workers. Most of the epithets were based on Schott names, but Engler treated most of these as varieties or subvarieties of *D. seguine* or *D. picta*. All of the taxa involved share a suite of characters that make it unique, namely the sharply sulcate petioles, the protruding and thickened staminate portion of the spadix, and bicarpellate ovaries.

A cultivated collection from Grenada (*Croat 77298*) had sap that was celery-scented, not at all smelling of oxalic acid, typical of so many *Dieffenbachia* species. *Croat 78323*, from Venezuela, also has a sweet- rather than a foul-scented sap.

Engler (1915) placed *Dieffenbachia lancifolia* Linden & André into synonymy with *D. picta*, but the former is a distinct species from Antioquia Department, Colombia. Also excluded are combinations of the name, *Dieffenbachia picta* Schott forma *lancifolia* (Linden & André) Engl. and *D. picta* Schott subvar. *lancifolia* (Lind. & André) Engl.

Also erroneously placed in synonymy with *D. picta* was *Dieffenbachia meleagris* Linden & Rodigas and the combination subvariety *meleagris* Engl. That species is from Ecuador (see illustration 159 in Ill. Hort.) and looks like it might be synonymous with *D. spruceana* Schott.

Dieffenbachia shuttleworthiana Engl. was synonymized with *D. picta* but should be excluded along with the following combinations: *D. picta* forma *schuttleworthiana* (Regel) Engl. and *D. shuttleworthiana* Hort. Bull. This Colombian species is not closely related to *D. seguine*.

Additional specimens examined. *André 1202* (K), *Cadet 6030* (K). BOLIVIA. **Pando:** Nicolas Suárez, a few km N of Cobija, *Beck 17103* (LPB, MO). **Santa Cruz:** Velasco, 10 km SE of buildings of Est. Flor de Oro, *Nee 41364* (MO, NY). BRAZIL. *Engler 226* (K, P), *Engler 227* (K, US). **Mato Grosso Sul:** *Catharino et al. 1909* (SP). **Pará:** Mpio. Capanema, Río Quatipuru, near Miraselvas, ca. 30 km by rd. W of Bragança, *Davidse et al. 18102* (MO); Río Anajás, Anajás-Vista Alegre, Cuanta do Anajás, *Beck et al. 295* (NY); Río Anajás, Ilha do Marajó, *Prance et al. 30247* (MO). **Rondônia:** Alta Floresta do Oeste, Rodovia P-50, *Gonçalves et al. 224* (MO). **São Paulo:** São Paulo, Instituto de Botanica de São Paulo, Secão de Fitoecologia, *Lotto s.n.* (K, MO). COLOMBIA. **Vaupes:** Río Kuduyari, tributary of Río Vaupes, *Schultes & Cabrera 17890* (NY). **Vichada:** Río Meta, Manati, *Cuatrecasas 4225* (US). ECUADOR. **Napo:** Auca Oil Field, *Ingram 1169* (MO, SEL). FRENCH GUIANA. Vic. of Saül, route to Béllizon, 100–300 m past Eaux Claires, *Croat 74137* (MO, US, VEN); Piste de Bélizon, pk 21.8, *Billiet et al. 6257* (MO); Crique Gabaret, bassin de l'Oyapock, *Cremers 9896* (CAY, K). **Cayenne:** Colline de Montravel, Ile de Cayenne, *Le Goff A. 95* (CAY, MO); Piste de Saint-Elie, 15.7 km S of ORSTOM camp, *Prevost 3258* (CAY, MO), *Prevost 3580* (CAY, MO); Centre ORSTOM de Cayenne, *Prévost 3382* (CAY, MO); Saint-Laurent-du-Maroni, Saül, trail to Mont Galbao, *Mori & Gracie 18717* (MO, NY). PERU. **Loreto:** Alto Amazonas, Dtto. Manseriche, Pongo de Manseriche, *R. Rojas et al. 607* (B, MO, US, WU). VENEZUELA. **Amazonas:** Río Guainia, S of Maroa, *Maguire et al. 36461* (NY); Cãno Mosquito, Cãno Marieta, *Lister & Colchester 272* (K); Tencua, *Colchester 2108* (K); Dpto. Atabapo, Río Cunucununa, Raudal Picure, *J. Pérez & M. Sosa 671* (MO); Cãno Majagua, *E. & S. Zent 2189* (MO); Casiquiare, Río Guainia, *Bunting et al. 4108* (NY); Dtto. Atures, Río Cataniapo, 45 km SE of Puerto Ayacucho, *Steyermark et al. 122412* (MO). **Apure:** Dtto. San Fernando, Río Arauca, 5 km SW of El Faro, *Davidse & González 13410* (MO). **Aragua:** betw. Maracay and Ocumare de la Costa, Henry Pittier NP, 1.6 km N of summit, *Croat 60567* (CM, F, MO); Pittier Park, Paraiso trail to Pico Periquito, *Croat 21412* (MO); Ocumare-Portachuelo, *Steyermark & Rogers 119364* (MO, USS); Portachuelo-Paraiso Trail, near Rancho Grande, *Bunting et al. 1937A* (NY); Rancho Grande to the Toma, *Bunting et al. 1949A* (NY); 12 km NW of Rancho Grande, *Bunting 2035* (NY), *Bunting 2036* (NY), *Bunting 2622* (NY); Maracay, campos de la Facultad de Agronomía y Centro de Investigaciones Agrícolas, Univ. Central de Venezuela, near Pozo del Diablo, *Bunting 2026A* (NY); vic. Maracay, *Bunting 2027* (NY); Río Tuy, NE of Maya, 7 km SE of Colonia Tovar, *Steyermark & Liesner 121834* (MO). **Bolívar:** La Gran Sabana, El Dorado-Santa Elena, km 202, S of Salto Kamá, *Davidse et al. 4844* (MO); base of Altiplanicie de Nuria, *Bunting & Holmquist 4319* (NY); W of Hato de Nuria, *Steyermark 88864* (NY, US); Río Karuai, base of Sororopan-tepui, W of La Laja, *Steyermark 60796* (NY); near El Paito, 5 km S of Caño Paso Ancho, *Bunting & Trujillo 2236* (NY); Kamarata, *Bogner 965* (M). **Carabobo:** PN San Esteban, Río San Esteban, *Benítez de Rojas et al. 4661* (MO, MY); Río San Gian, 5–6 km S of Borburata, *Steyermark 94331* (MO, US). **Delta Amacuro:** Río Amacuro between "vuelta larga" and Cerro Wuausa, Dept. Antonio, *Trujillo et al. 17397* (MY). **Distrito Federal:** Fila Las Delicias above Naiguatá, *Bunting & Manara 2124V* (NY), *Drake 7* (P, US); Cerro Naiguatá, 6 km SW de los tanques de la Electricidad de Caracas (Cocuizal), *Steyermark 91896* (NY, US); Los Caracas-Higuerote Rd., between km 5 and Osma, *Bunting & Fernandez 3295* (NY); Pico Naiguatá, Fila Las Delicias Naiguatá, vic. Las Delicias, *Bunting & Manara 2126* (NY), *Bunting & Manara 2119* (NY); Río San Julián, just above Caraballeda, *Bunting 2044* (NY). **Falcón:** PN Quebrada de la Cueva El Toro, *Liesner et al. 7681* (MO). **Lara:** Dtto. Jiménez, PN Yacambú, Quebrada Negra, *Davidse & González 21012* (MO). **Miranda:** Cerros del Bachiller, 5.5 km S of village Santa Cruz on Hwy. 9 between Guatire and Cupira, *Croat 53956* (MO); Cerros del Bachiller, near E end, 10 air km W of Cúpira, *Steyermark & Davidse 116647* (MO); PN Guatopo, Fila la Guzmanera, Santa Teresa-Altagracia de Orituco, ca. 8 km S of jct. of rd. to Caucagua, *Bunting et al. 2072* (NY), *2074* (NY); Sta. Teresa-Altagracia de Orituco, *Aristeguieta 1764* (NY), *Croat 21741* (MO); Caucagua, 600 m, *Bunting et al. 2073* (NY). **Monagas:** Morichal Las Tetas, tributary of Río Tonoro, near Aguasay, *Montes s.n.* (MO); Caripe-Santa Ines Rd., ca. 3 km E of Teresen, Colorado-Los Cigarrones, Río Colorado, *Bunting 2729* (NY); Jusepín-Barcelona Rd., 6 km SW of Jusepín, *Bunting 2738* (NY); Caripe-Maturín Rd., *Bunting 2678* (NY); Morichal El Esfrerzo, Jusepín, *M. Heredia 60* (MO). **Nueva Esparta:** Margarita Island, Juan Griego trail, *J. R. Johnston 305* (NY, US). **Portuguesa:** Quebrada Algarrobo, tributary of Río Morador, 7 km NE of Boca de Monte, 22 km NE of Río Suruguapo, *Steyermark et al. 127204* (MO); Guanare-Biscucuy Rd., El Puente, 21 km above jct. of Guanare-Barinas rd., *Bunting 3321* (NY); Dtto. Araure, Río Auro (La Lucia), NW of Sta. Lucia, *Aymard & Ortega 3090* (MO); Dtto. Guanare, Guanare-Barinas, Mpio. Mesa de Cavacas, *Stergios et al. 7940* (MO, PORT). **Sucre:** El Pilar-Guariquén, El Pilar and Guariquén, 4–10 km S of El Pilar, *Croat 54380* (MO). **Táchira:** 8 km S of El Pinãl, *Steyermark et al. 102036* (MO, MY); San Cristóbal-Chorro del Indio, Caño Secto-La Florida, km 14–20 al E de San Cristóbal, *Bunting 11687* (MO); vic. Las Minas, N of La Laguna, 16 km SE of Santa Ana, *Steyermark & Liesner 118891* (MO). **Trujillo:** Sabana-Mendoza, ca. 5 km below Betijoque, *Bunting 2829* (NY). **Yaracuy:** Las Trincheras-El Cambur, N of Salom (NE of Nirgua, W of Valencia) on rd. to Candelaria, *Croat 54649* (CM, MO); Marín and Aroa, Sierra de Aroa, Dtto. Felipe between Albarico and Tesorero, 9.8 km N of jct. of hwy. 1 at Marín, *Croat 60613* (MO); Sierra de Aroa, PN Yurubí, 0–2 km N of San Felipe, Río Yurubí, *Liesner & A. González 10126* (MO, NY); Sierra de Aroa, vic. Aracal, 7 km above San Felipe, *Bunting et al. 1997* (NY); Cerro La Chapa, N of Nirgua, *Steyermark & Bunting 97728* (NY); Dtto. Nirgua-Dtto. San Felipe, Cerro La Chapa, 7 km N of Nirgua, *Davidse et al. 20914* (MO); Cerro La Chapa, *Steyermark et al. 100213* (NY, US); Cerro La Chapa, *Steyermark et al. 100318* (US), *Steyermark et al. 100239* (US); Dtto. Nirgua, Salom-La Candelaria Rd., Cumbre Gamelotal, *Meier et al. 5164* (MO, VEN); Dtto. Bruzual, Montaña de María Lionza, W of Sorte, *Steyermark et al. 124955* (MO); Dtto. San Felipe, PN Yurubí, *Aymard et al. 2714* (MO); Dtto. Urachiche, Quebrada Higueronal, W of Urachiche, vic. Sabana de Méndez, *Steyermark et al. 124629* (MO); Río Guayabito, 15 km N of Marín, *Steyermark & Bunting 105293* (MO). GREATER ANTILLES: HAITI. *Nash 611* (NY); massif de la Lelle, Port au Prince, Mantflurry, *Ekman 1983* (K). HISPAÑIOLA. SANTO DOMINGO. **San Cristóbal:** Cordillera Central, San Cristóbal, Hato Damas-Mano Matuey, *Croat 68582* (MO). **Barahona:** *Fuertes 564* (GH); Santo Domingo, *Zanoni et al. 27170* (GH, MO, NY); El Aguacate, La Leonor, Moncion,

Liogier 13307 (GH, NY); Carib Territory, Bataka, *J. Higgins 119* (MO, NY); Sierra de Baoruco, Arroyo La Travesia near the La Travesia sugar mill, *Zanoni et al. 25159* (MO, NY). **El Seibo:** El Guaraguao-Los Hurados, Miches-Higuey, km 15, *Mejia & Ramirez 9929* (MO, NY). **Monseñor Nouel (Peravia):** Cordillera Central, Río Yuboa, *Zanoni et al. 23113* (MO, NY); Cordillera Oriental, Arroyo de Agua, 11.7 km W of El Valle, *Croat 68494* (MO); 9.2 km SE of Miches, along Río Yeguada, Arroyo Santiago, *Croat 68547A* (JBSD, K, MO). **Samana:** 2.3 km S of Playa El Valle, *Mejia & Zanoni 6614* (MO, NY); Sanchez, Las Canitas Mts., *N. Taylor 48* (NY); Sanchez Ramirez, *Rose et al. 4375* (NY); Río Cevicos, W of Cevicos, 22 km E of Cotuí, *Zanoni & Pimentel 23420* (MO, NY). **San Cristóbal:** San Cristóbal, a Jina (de Yamasa), 16 km del Parque Central de Yamasa, *Zanoni & Pimentel 23456* (MO, NY); near Río Nigua, *Lavastre 1845* (NY); near Nigua River, La Toma, *Augo 1693* (NY); El Dajao, Bayaguana, *Liogier & Liogier 20185* (NY). JAMAICA. **Port António:** *Hitchcock s.n.* (MO); Fury River, *Harris 8361* (NY); John Crow Mts., *Britton 4126* (NY). **Portland:** foothills of John Crow Mts., W of Ecclesdown, *Grayum et al. 9973* (K, MO). **St. Elizabeth:** Frenchman, *Proctor 38601* (NY). PUERTO RICO. Without exact locality: *Engler 2793* (K), *Sintenis P. 2793* (K), *Britton & Britton 9664* (NY), *Britton & Britton 7897* (NY); Maricao, *Sargent 643* (MO); San Sebastian, *Sargent 340* (MO); Laguna Tortuguero, *Howard & Nevling 16978* (A); Quebrada Prieta, El Verde Field Station in Luquillo Experimental Forest, W side of Luquillo Mts., *Whitehill 8* (MO); Luquillo Mts., Palmer-Florida, km 28.1, *R. Wagner 558* (A); Río Abajo State Forest, Hwy. 621, *Croat 60867* (MO, NY, PMA, RSA); km 21.5 on Rte. 2, W of Candelaria, *Solomon 5761* (MO); Mayaguez vic., *Cowell 550* (NY), *Britton & Shafer 1625* (NY), *Britton & Britton 10082* (NY); Mpio. Maricao, Bo Indiera Fria, Rt. 425, 0.3 km S of Rt. 105, *Atha & Zanoni 770* (MO); Coamo, *Woodbury et al. s.n.* (MO); Caribbean Nat. For., ca. 1 km N of Río Sonadara, Hwy. 186, *Thompson 3238* (MO); Mpio. Lugillo, Route 988, 1 mi. E of intersection with rt. 983, *Miller & Taylor 5937* (MO); Río Piedras, *Cowgill 532* (NY). LESSER ANTILLES: VIRGIN ISLANDS. **St. John:** N Bordeaux Mountain, Coral Bay Quarter, 100 m from communications tower, *Acevedo-Rodríguez 4705* (MO, NY). **Tortola:** Carrot Bay, *D'Arcy 769* (MO), *Fishlock 326* (K). ST. KITTS. *Britton 447* (NY). LEEWARD ISLANDS: DOMINICA. Roseau-Sulfur Springs, *Howard 11744* (A); N of Calibishie, *Hodge & Hodge 3174* (GH); Milton Estate, *Hodge 2929* (GH); Castle Bruce Valley, *Beard 656* (GH); St. Patrick Parish, Cote d'Or, *Nicolson 2060* (GH), *Lloyd 237* (NY); St. Mark Parish, Sulphur Springs area, *S. Hill 24812* (NY). GRENADA. Near Mt. Horn, towards Birch Grove, *Simmonds s.n.* (K). GUADELOUPE. **Guadeloupe:** *Duss 3790* (NY, US); Admdiv. Basse Terre, Piste vers 3e chute de Carbet, *F. Billiet & B. Jadin 7359* (BR, MO); Basse Terre, Grande Etang (Près des chutes du Carbet), *Billiet & Jadin 7357* (MO), *Billiet & Jadin 7358* (BR, MO); Basse Terre, Crique Lézarde, *Billiet & Jadin 7346* (BR, MO), *Billiet & Jadin 7347* (MO). **Marie Galante:** ravine of Riviere de St. Louis, Grand Bassin-Les Balisiers, *Proctor 20987* (A, US). WINDWARD ISLANDS: MARTINIQUE. *M. Hahn 945* (GH, K, P, US), *P. Duss 21496* (NY). ST. LUCIA. *Sturrock 352* (A); Anse Louvet near nursery, *Slane 634* (A), *Howard 11564* (A). ST. VINCENT. *H. H. Smith & G. W. Smith 1411* (K, NY). TRINIDAD. Arima-Blanchisseuse rd., at mi. 4, *Croat 53921* (HUA, K, MO, NY, TRIN, VEN); Arima-Blanchisseuse Rd., near milepost 7 ¾, *Philcox 8231* (K).

Cultivated specimens. Society Islands. Leeward. Raiatea Island, cultivated in Uturoa, 17 Dec. 1926, *J. W. Moore 451* (MO). U.S.A. Hawaii: Honolulu, Kalihi Valley, 15 Mar. 1956, *Harris & Neal s.n.* (BISH); Foster Gardens, 3 Mar. 1962, *Miyashiro s.n.* (BISH); Lyon Arboretum, 10 Sep. 1975, *D. Herbst & S. Ishikawa 5459* (BISH); Oahu, 5 May 1954, *Won s.n.* (BISH); Honolulu, Kaimuki, 5 May 1954, *R. Won s.n.* (BISH); Kapalama Heights, Kamehameha Girls School, 6 June 1932, *Judd et al. s.n.* (BISH). Missouri: Missouri Botanical Garden, originally obtained from J. Henny, Apopka, *Henny 7* (MO), *Croat 78287* (MO); 13 Sep. 1990, *Miller & Schmidt 5551* (MO). Puerto Rico. Río Abajo (originally collected by *Thompson 3238*), 19 June 1997, *Croat 78345* (MO). Hispañiola. Border of PN Los Haitises, 27 Apr. 2000, *Luther s.n.* (*Holst 6237*) (MO). Grenada. Originally collected by John Criswick, Grenville, Grenada, 1993, *Croat 77298* (MO, VEN). Belize. Cayo: Nabatunich, near Sukkotz, 17°06′N, 89°W, 24 Jan. 1990, *Balick et al. 2359* (MO). Venezuela. Carabobo: originally collected by Bunting from a Garden in Valencia, 300–500 m, (*Bunting 13515*) *Croat 78323* (MO, VEN); Jardín Botánico, Caracas, 19 Aug. 1976, *Croat 38344* (MO).

24. Dieffenbachia standleyi Croat, sp. nov. TYPE: Honduras. Lancetilla Botanical Gardens, ca. 2 mi. WSW of Tela and S of main hwy., 15°44′N, 87°27′W, 70–90 m, 9 Feb. 1987, *T. B. Croat & D. Hannon 64638* (holotype, MO-3442883!; isotypes, B!, CAS!, COL!, EAP!, F!, GH!, INB!, K!, MEXU!, PMA!, NY!, TEFH!, US!, USCG!). Figures 24, 28B.

Planta 0.6–1.5(3.0) m alta; internodia 3–6(10) cm longa, 6–11 cm diam.; petiolus 12.5–52 cm longus; lamina elliptica vel obovato-elliptica, 31–84(103) cm longa, 12.5–39 cm lata, nervis primariis lateralibus 12–24 utroque; inflorescentia 2–4 per axillam; pedunculus ad (7.5)15–29 cm longus; spatha 20–50 cm longa.

Terrestrial herb, frequently in streams or on stream banks, 0.6–1.5(3.0) m tall; sap foul-smelling, caustic and irritating; *internodes* 3–6(10) cm long, 6–11 cm diam., dark green, semiglossy; *petioles* 12.5–52 cm long (averaging 26 cm long), matte, light green, paler than stem, finely and densely striate throughout, sheathing nearly always to the base of the blade, the margin usually markedly undulate and thin, sometimes with the apical portion curled outward, otherwise erect, often drying undulate, free unsheathed portion 1–5 cm long (averaging 2 cm long); *blades* elliptic to obovate-elliptic, 31–84(103) cm long, 12.5–39 cm wide (averaging 54 × 23 cm), 1.7–3.1 times longer than wide (averaging 2.5), 2.1–4.6 times longer than petiole (averaging 3.2), inequilateral, one side 3–4 cm wider, abruptly acuminate at apex, somewhat inequilateral and acute to weakly attenuate or rounded to obtuse at base, coriaceous, dark green and semiglossy to glossy above, paler green and matte below, drying medium gray to dark brownish gray above, paler and yellowish gray to pale yellow-

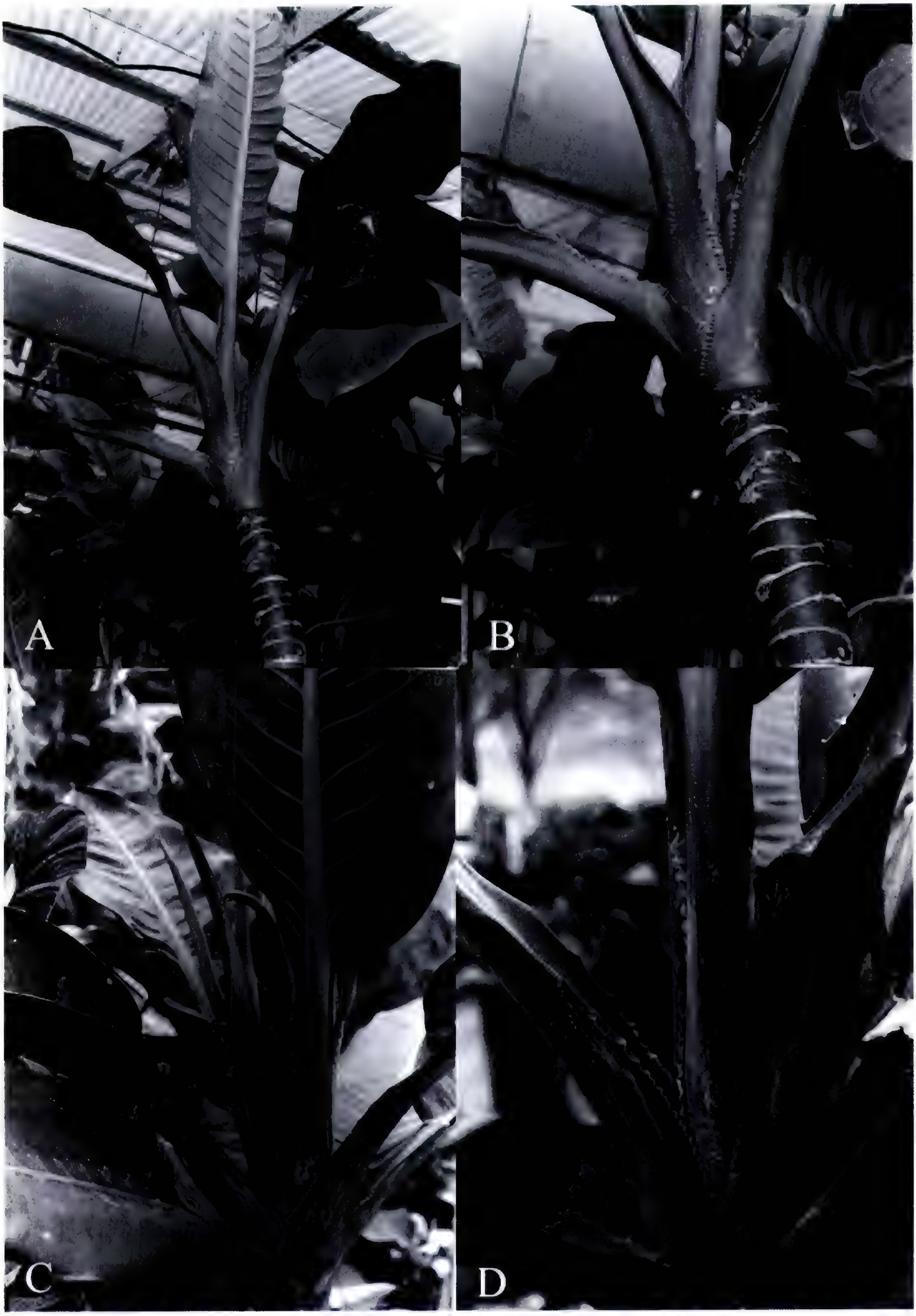


Figure 24. *Dieffenbachia standleyi* (*Croat 42676*). —A. Habit of cultivated plant. —B. Stem and base of leaves. —C. Upper part of stem showing abaxial surface of leaf blade and cluster of inflorescences. —D. Close-up of petiole bases showing the markedly undulate petiole sheaths.

brown below; *midrib* slightly paler and flat to sulcate and finely paler striped above (especially near the base), sometimes white in distal ⅔, convex to narrowly rounded, thicker than broad and paler to slightly paler below, drying 8–12 mm wide, medium yellow-brown, finely ribbed with the ribs minutely and obscurely scabridulous on magnification; *primary lateral veins* 12 to 24 per side, arising at an acute angle, then spreading at 40°–65°(70°) angle, obtusely sunken and weakly quilted, paler toward midrib above, bluntly angular and ± concolorous below, drying pale yellow-brown; lower surface with minor veins moderately obscure, arising mostly from the midrib but also from the primary lateral veins. INFLORESCENCES 2 to 4 per axil; *peduncle* to (7.5)15–29 cm long (averaging 16 cm long), somewhat flattened; *spathe* matte, 20–50 cm long (averaging 28.3 cm long), 1.2–3.1 times longer than the peduncle (averaging 1.6 times longer), 2.5–3.0 cm diam.; *spadix* 20–30 cm long (averaging 25 cm long); pistillate portion of spadix 12–13 cm long; staminate portion 15–16 cm long. Fruits to 1 cm long, closely packed, reddish orange to scarlet at maturity with the spathe light yellow.

Distribution and habitat. *Dieffenbachia standleyi* ranges from Honduras (Atlántida, Comayagua, Cortes, El Paraíso, Gracias a Dios, Olancho, Yoro) to Nicaragua (Matagalpa and Zelaya) at 30–1000 m elevation. Most collections in Honduras were made in the Lancetilla Valley.

Phenology. Flowering specimens of *D. standleyi* have been seen from May through September, although a few flowering collections were also made as early as February and March. Fruits start to develop in February and reach full size during March or April (in Nicaraguan collections) or July–August (in Honduras).

Discussion. The species is characterized by its stout stem, fully winged petioles, yellow-brown-drying ovate-elliptic blades with 12 to 24 pairs of primary lateral veins, and a long spathe (20–50 cm). It is most easily confused with *D. horichii* and may ultimately prove to be inseparable from that species. *Dieffenbachia horichii* differs in having shorter petioles with the sheath involute and moderately smooth, in contrast to the petiole sheaths erect and even curled outward as well as being undulate along the margins in *D. standleyi*.

A collection by *Stevens et al. 20998* from Matagalpa is unusual in being described as 3 m tall with a trunk 10 cm in diameter. Another Stevens collection (*7457*) from Zelaya Department is noteworthy in drying darker yellow-brown than other collections.

Specimens from Nicaragua differ somewhat from those in Honduras, having leaf blades smaller on average, ranging from 37 to 69 cm long and 13 to 31 cm wide (averaging 51 × 22.3 cm), but the petioles in both areas average 30 cm long. The Honduran populations have petioles consistently fully sheathed, whereas plants in Nicaragua often have a free portion of the petiole above the sheath ranging from 1 to 9 cm (averaging 4.4 cm long) with the petioles only rarely fully sheathed.

Blade shape is quite variable. Blades can be from 1.9 to 2.8 times longer than wide on the same plant (e.g., *Croat & Hannon 64638*). Plants from the Lancetilla Valley in Honduras have proportionately longer blades, with some plants having blades up to 3.2 times longer than wide (*Croat 42676*). Specimens collected at Lancetilla and its surroundings have blades that range from 1.9 to 3.5 times longer than wide (averaging 2.5 times longer than wide). Specimens from areas other than Lancetilla, and outside Honduras, have blades 1.6 to 2.7 times longer than wide (averaging 2.1 times longer than wide).

A collection from Zulia, Venezuela, between La Fría and San Juan de Colón (*Croat 78289*) differs in having the petiole less fully sheathed and in having narrower blades up to 2.6 times longer than broad and drying somewhat less blackened. It may prove to be the same species. If so, it would be the only Central American species (with the possible exception of *D. killipii*) that ranges from Central America to Venezuela.

Etymology. *Dieffenbachia standleyi* was first collected in 1928 by Paul Standley at Lancetilla, Honduras. Standley was not only the author of most of the aroid treatments for most existing Central American floras, but he also described a number of new species of Araceae, as well as collecting several paratypes of *D. standleyi*. The species is named in his honor.

Paratypes. HONDURAS. **Atlántida:** 5 km S of La Ceiba, *Madison 705* (GH); near Lancetilla, *Yuncker 4961* (F, MO, NY); Lancetilla valley, near Tela, *Pfeifer 2124* (US); near Puente Alto stop on S.F. Co. R.R., E of Ceiba, *Yuncker et al. 8551* (F, GH, MO, NY, US); ca. 3 mi. S of Tela, *Webster et al. 12581* (DAV); vic. Tela, near Río Lancetilla, above Exp. St., *MacDougal et al. 3303* (MO, NY, US); Tela, ca. 10 mi. SE of Tela along Río Lancetilla, *Croat 42625* (MO), *Croat 42676* (MO), *Standley 53146* (F, US). **Comayagua:** Siguatepeque, *Standley & Chacón 6701* (F). **Cortes:** 2–3 mi. SW of Omoa on rd. from Puerto Cortes to Guatemalan border, *Croat 42556* (MO); El Paraíso, Yuscarán, Río de los Aguacates, *Standley 25700* (EAP). **Gracias a Dios:** Ahuas Bila, 200 km SW of Puerto Lempira, *Nelson & Cruz 9291* (TEFH, UNAH, US). **Olancho:** Catacamas, *Standley 18786* (EAP); along Río Olancho, W of main Tegucigalpa-Catacamas Hwy., ca. 1

km upstream from and NW of Puente Boquerón, 8.6 mi. SW of Catacamas, 6 mi. SW of Sta. María del Real, *Croat & D. Hannon 64109* (INB, MEXU, MO, TEFH, US); along Río Olancho, on rd. Gualaco–San Esteban at Río San Martín, 19.3 mi. E from Gualaco, 8.7 mi. SW of San Esteban, *Croat & D. Hannon 64317* (B, MO, US); Río Olancho, San Esteban-Bonito Oriental, 19 mi. NE of San Esteban, *Croat & D. Hannon 64476* (MO); Refugio de Vida Silvestre "La Muralla," *Nelson & Andino 16247* (TEFH); Mpio. Jano, 16 mi. NE of La Unión along the rd. to Olanchito, *Davidse et al. 35484* (MO). **Yoro:** near Puente Grande, on a tributary of the Río Agua (Río Puente Grande), *Blackmore & Chorley 4073* (MO). NICARAGUA. **Matagalpa:** El Toma Rd., *Neill 1571* (MO); ridge along rd. betw. La Danta and La Luna, E of Esquipulas, *Stevens 11786* (CAS, MO, TEX); Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradon, Hda. San Martín, border with Departmento de Jinotega, *Stevens et al. 20998* (MO); Matagalpa-Siuna, 1.5 km al NE de Los Angeles, *Moreno 17142* (MO); El Trébol, 7 km S of Peñas Blancas, rd. to El Tuma, *Moreno & Robleto 20526* (MO). **Zelaya:** Finca Waylawas, *Pipoly 4479* (MO, US); Siuna-Matagalpa, ca. 31.4 km beyond Río Ulí (near Waní), ca. 8.9 km beyond Rosa Grande La Balsama, *Stevens 7457* (MEXU, MO); Cerro Livico, 7 km NE of Siuna, *Neill 3629* (MO); Río Sucio, E of Bonanza, *Stevens 12311* (MO), *Stevens 8044* (MO); Res. Bosawas, Bonanza, Cerro Cola Blanca, vic. Cacerio de Vitinia, *Rueda & Coronado 6557* (MO).

25. Dieffenbachia tonduzii Croat & Grayum, Novon 9: 497. 1999. TYPE: Panama: Bocas del Toro: Valle del Silencio, along Río Changuinola, ca. 1 km above mouth of Río Teribe, vic. Teribe Indian population, disturbed forest among cocoa plantations, 9°21′40″N, 82°31′40″W, less than 100 m, 25 June 1994, *T. B. Croat & G. Zhu 76452* (holotype, MO-04611212!; isotypes, AAU!, B!, BM!, BR!, CAS!, CM!, COL!, CR!, DUKE!, F!, GH!, HUA!, INB!, ITIC!, JAUM!, K!, L!, LE!, M!, MEXU!, NY!, P!, PMA!, QCA!, QCNE!, R!, RSA!, S!, SCZ!, SEL!, TEX!, UB!, US!, VEN!, WU!). Figures 25, 29B.

Terrestrial herb, 0.5–1.5 m tall, usually to less than 1 m tall; *internodes* 1.5–4.5(–6) cm long, 1.5–3(–4.5) cm diam., usually solid dark to medium green, sometimes faintly marbled with gray-green or yellowish gray throughout (on plants that also have streaked petioles), initially weakly glossy, becoming semiglossy to glossy, often with a subvelvety sheen; petiole scars manila to white, curved downward on the opposite side of the stem and ending unevenly; *petioles* 10–24 cm long (averaging 17.6 cm long), held ± erect, medium green (except sometimes white to pale green at base), almost matte to weakly glossy, weakly striate (especially near the base), narrowly rounded to obtusely angular on abaxial surface and often white medially, sometimes streaked in a variegated pattern throughout (this white coloration continuing onto the midrib), sheathed virtually throughout; sheath erect to involute (rolled inward throughout in age), free-ending and unequally rounded at apex, prolonged to 2 cm beyond the base of blade; unsheathed part obsolete or rarely to 1 cm long (when evident obtusely flattened); *blades* ovate to ovate-elliptic or oblanceolate-elliptic, (15–)25–48(–63) cm long, (8–)15–32 cm wide (averaging 34 × 16 cm), broadest near the middle, sometimes below, frequently above the middle, 1.4–2.5(–3.5) times longer than wide (averaging 2.1 times longer than wide), 1.9–3 times longer than petioles, spreading to erect-spreading, inequilateral, one side 1–3 cm wider than the other, gradually to abruptly acuminate, sometimes acute at apex, inequilaterally cordulate at base, one side sometimes broadly rounded to obtuse, the other side cordulate, sometimes inequilaterally acute, subcoriaceous, often conspicuously quilted, moderately bicolorous; upper surface usually solid dark to medium green, sometimes conspicuously to sparsely variegated with pale green or pale yellow throughout much of the surface, the mottling large or small, but somewhat restricted to the area midway between the midrib and margin, matte to weakly glossy, sometimes appearing weakly velvety, drying gray-green to olive-green or dark brown; lower surface much paler and matte to weakly glossy, silvery-green, drying yellowish green to yellow-brown below; *midrib* flat to broadly rounded and moderately to strongly paler, pale green or sometimes creamy white above (sometimes only toward the apex), bluntly acute to obtusely angular and paler, sometimes white or creamy white below, (0.6–)1–1.7 cm wide; *primary lateral veins* (14 to)18 to 25(to 30) per side, arising at an acute angle and spreading at 45°–90°, sometimes reflexed toward the base, prominently to weakly and obtusely sunken above, convex to weakly raised and darker than surface or concolorous below, some of the lowermost with a weak fold near the base (*Croat & Grayum 60112*), sometimes convex-pleated below; interprimary veins almost as conspicuous as the primaries; minor veins moderately to distinctly visible, darker than surface below. INFLORESCENCES 1 to 2(to 4) per axil, often with two oriented in opposite directions; *peduncle* (3–)6–17 cm long (averaging 10.3 cm long), 7–8 mm diam., weakly glossy, dark to medium green, sometimes with pale yellow-green streaks; *spathe* (12–)15–28 cm long (averaging 20 cm long), 2–4 times as long as peduncle, acuminate at apex, convolute to about the middle in lower part, matte to weakly glossy outside, glossy within, solid medium green on both surfaces, gradually and weakly constricted some-

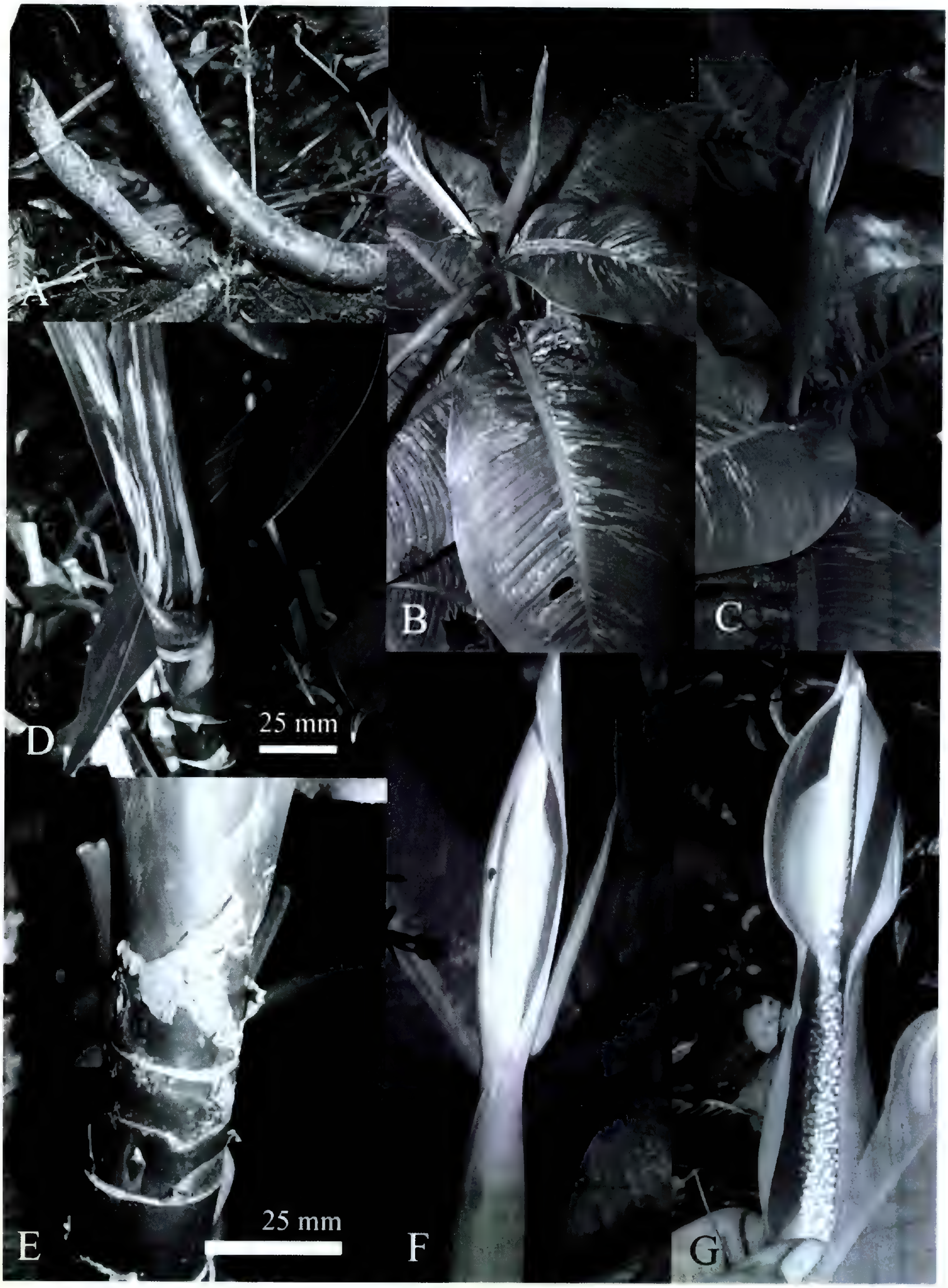


Figure 25. *Dieffenbachia tonduzii.* —A. Close-up of stem, showing both creeping and erect portions. —B. Habit with inflorescences and variegated blades. —C. Crown of plant with open inflorescence. —D. Close-up of stem showing petioles streaked with creamy white. —E. Close-up of stem showing solid green petioles. —F. Close-up of spathe with the blade portion open (*Croat & Zhu 76452*, type plant). —G. Inflorescence open to show upper male flowers and lower portion of spadix with pistils and staminodia (*Croat 66533*). A, B, C. (*Croat & Zhu 76452*, type plant); D, E. (*Croat 76450*).

what above the middle; spathe tube 1.5–3 cm diam. when closed, 6.8–9 cm wide when flattened; constricted area 4.3–4.5 cm wide flattened; *spadix* (9–)16.5–25.5 cm long, about as long as or up to 3.0 cm shorter than the spathe; free portion 7.8–8.5 cm long; pistillate portion (4.8–)6–11.5 cm long; mostly sterile portion sparsely flowered to naked (rarely lacking, as in *Croat 70768*), 1.8–4.0(–8.5) cm long with 0.6–1.5 cm totally bare, the uppermost portion with a few staminodia, sometimes with a few scattered staminodia throughout, the lower half sometimes with an occasional pistil and much reduced staminodia, rarely with the female flowers ± equidistant and nearly contiguous with staminate part (*Croat 70768*); fertile staminate portion (4–)5.5–10 cm long, 7–10 mm diam., slightly broader midway, weakly tapering to apex and base, bluntly pointed at apex; staminate flowers 5 to 6 per spiral, ± rounded in outline, crenulate along margins, truncate at apex; sterile male flowers irregularly shaped, 1.8–2.5 mm diam.; pistillate portion of spadix to 11 cm long, 9–10 mm diam.; female flowers (15 to)48 to 62, closely aggregated except in the upper 1.5 cm of spadix, 4 to 5 across the width of the spadix (uppermost pistil borne on an almost bare segment of the spadix); pistils pale cream-yellow to pale yellow-green, smooth, 2.3–3.5 mm diam.; style (after stigma has fallen) sharply cupuliform, 1.5–1.7 mm diam. with a single central pore; stigmas yellow; staminodia clavate, white, 2–3 mm long, mostly contiguous and sometimes fused at base. INFRUCTESCENCES with spathe pale yellow; *berries* red to red-orange, 5–8 mm diam.

Distribution and habitat. *Dieffenbachia tonduzii* ranges from southeast Nicaragua throughout Central America to the Pacific slope of Colombia (Antioquia, Chocó, Cauca, Valle) and Ecuador (Esmeraldas, Loja, and Los Ríos), from sea level to 1400 m, in *Tropical wet forest* (T-wf) and *Premontane rain forest* (P-rf) in Central America and in *Tropical wet forest* (T-wf) and *Premontane wet forest* (P-wf) and *Tropical wet forest* transition to *Premontane* (T-wf/P) in Colombia.

Phenology. Flowering in *D. tonduzii* occurs throughout most of the year with flowering collections seen from February through November. Most collections have been made from April through August. According to the collections, fruits mature throughout the year but with the greatest concentration from October to January.

The species is characterized by its fully sheathed petioles, usually matte to weakly glossy, sometimes weakly velvety blades with cordulate bases and numerous, broadly spreading primary lateral veins. Because of the fully sheathed petioles it can be confused only with *D. horichii* and *D. crebripistillata.* Both of the latter typically have much larger leaves that are not at all cordulate at the base (though they are rarely broadly and weakly subcordate). *Dieffenbachia tonduzii* is polymorphic with regard to leaf markings in the same way as *D. oerstedii,* and is quite variable in all respects. It appears, in Panama, to hybridize with *D. oerstedii. Croat & Zhu 76857C* from the vicinity of Santa Fé in Veraguas Province is apparently a hybrid with characteristics intermediate between *D. tonduzii* and *D. oerstedii.*

The species is similar to *D. daguensis,* a Colombian species described from less than 200 m elevation on the Río Dagua in Valle Department. That species also has many rather close primary lateral veins and a fully sheathed petiole but differs in having the staminate and pistillate sections of the spadix contiguous or nearly so. In addition, it differs in having much shorter petioles (described as being up to 5 cm long).

A South American species, *D. parlatorei* Linden & André, also sometimes has petioles fully sheathed, but differs from *D. tonduzii* in having leaf blades usually broadest above the middle, semiglossy on the lower surface, and the midrib often broadly rounded and spongy. It also has the primary lateral veins arising at a 40°–60° angle from the midrib (often at more than 60° and sometimes up to 90° in *D. tonduzii*).

Croat 70900, from 250 m in Chocó Department of Colombia, appears to be *D. tonduzii* but differs in several ways. It has leaves with the midrib flat-raised above with the margins undercut. It also has stems that appear scurfy (though weakly glossy if rubbed clean). Another difference is that the petiole sheath is more prominently free-ending and subacute at the apex. In addition, the free portion of the petiole is broadly and sharply sulcate.

Additional specimens examined. COSTA RICA. **Alajuela:** rd. to Colonia Virgen del Socorro, Río Sarapiquí, *Stevens 13564* (MO), *Croat 68336* (CR, MEXU, MO, TEFH); Cantón de Alajuela, *Grayum & Murakami 9939* (CR, MO); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, *Croat 43629* (CM, MO); Cañas-Upala, 10 km N of Bijagua, *Croat 36472* (MO); Río Zapote, Cañas-Upala, Río Zapote, 4 km NNE of Bijagua, *Croat 36260* (MO); Cordillera de Tilarán, San Ramón-Bajo Rodríguez, Río Cataratitas, *Croat 68097* (INB, MO); Cordillera de Tilarán, San Ramón-Bajo Rodríguez, vic. of km 19.5 NW of San Ramón, *Croat 78838* (MO); 17–20 km NNW of San Ramón by rd. on way to San Lorenzo, 4–7 km N of Balsa, *Liesner & Judziewicz 14797* (CR, MO); San Ramón-Bajo Rodríguez, 36–37 km NW of San Ramón, *Croat 68196* (CM, MO, W); Naranjo-Aguas Zarcas, along Hwy. 15, 8 km NE of Quesada, *Croat 46945* (K, MO, PMA); Arenal Volcano, *Funk et al. 10626* (CR, US), *Funk et al.*

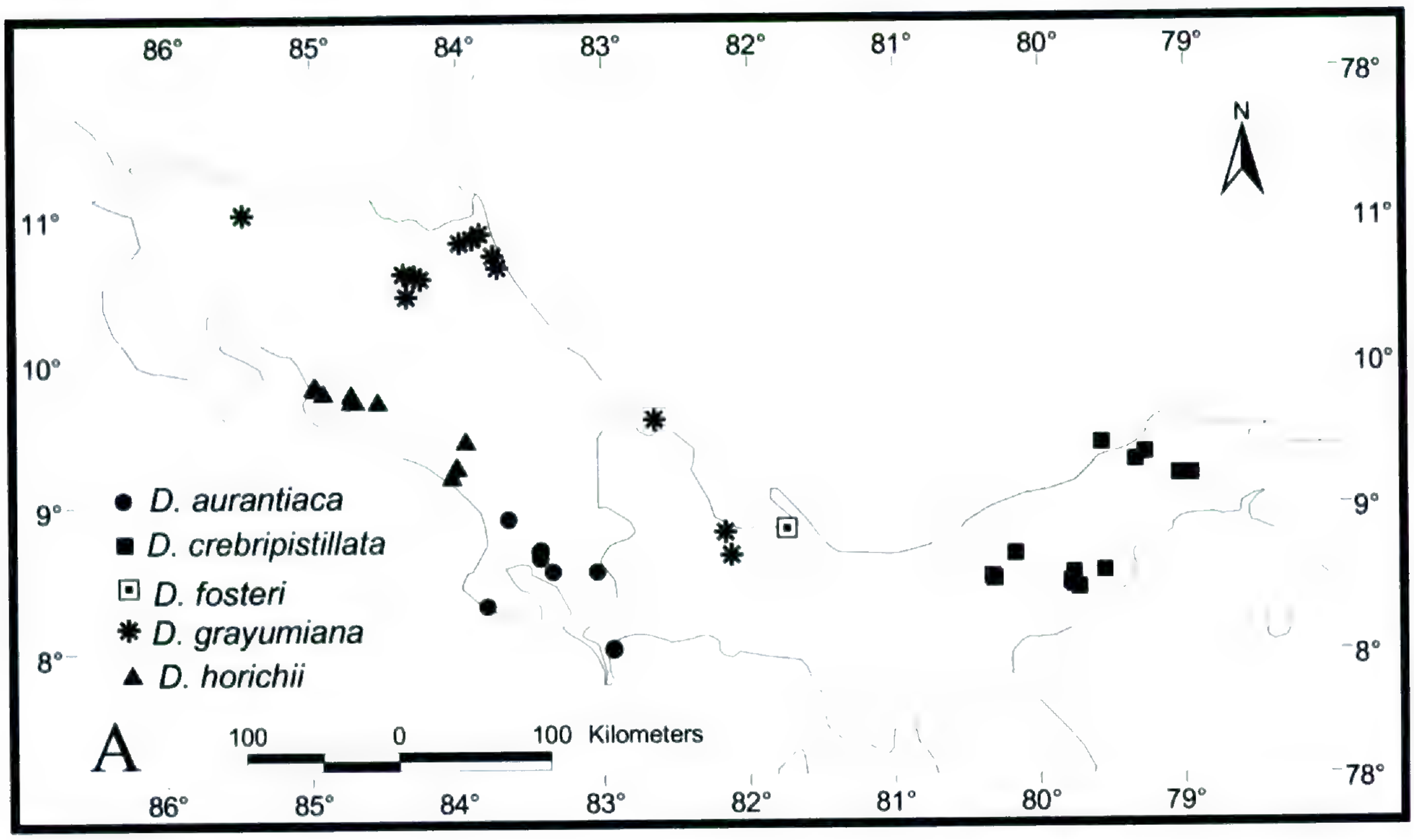
10718 (CR); San Ramón-Fortuna, ca. km 25, *D. Smith et al. 1059* (DUKE, MO); Cordillera de Guanacaste, Monteverde, San Gerardo Biol. Sta., 1.5 km NE of Station, *D. Penneys 633* (CR, INB, MO); Cordillera de Tilarán, Bosque Eterno De Los Niños, Río Peñas Blancas, Laguna Poco Sol, *Haber & Zuchowski 11175* (CR, MO). **Cartago:** Tucurrique, *Tonduz 12874* (G, US); Río Naranjo, Finca El Cedral, Orosí, *Lent 4042* (F, MO, NY, SEL); La Vuelta, Tucurrique, *Tonduz 503* (US); 1.5 mi. E of Cachi, 10.2 mi. NE of jct. at Paraíso, *Croat 47088* (MO); along Camino Raiz de Hule, SE of Platanillo, *Croat 36727* (MO), *Croat 36747* (MO), *Croat 36821* (MO); Cantón de Turrialba, Río Reventazón, CATIE, Turrialba, *Grayum et al. 9469* (CR, MO, NY); 3 km E of Turrialba "Los Espaveles" nature trail, Río Reventazón, *Liesner et al. 15330* (MO); Turrialba, Instituto Interam., *Lent 639* (F), *Lent 694* (F); 12 km S of Turrialba by air, 4 km SE of Pejibaye along Río Gato, *Liesner 14394* (MO); Tres Equis, 1.5 km E of Turrialba-Limón Hwy., *Liesner et al. 15365* (MO); PN Tapantí, Oropendola trail, *Nilsson et al. 632* (CR); Oropendola trail, *Nilsson et al. 377* (CR); Monumento Nacional Guayabo, *Pérez 1* (CR); Monumento Nacional Guayabo, Santa Teresita, *Rivera 1718* (CR, K). **Guanacaste:** El Arenal, *Standley & Valerio 45262* (US); El Real, *Standley & Valerio 45206* (US); Cordillera de Guanacaste, Rincón de la Vieja, near refugee camp, along rd. NW of Quebrada Grande, *Barringer et al. 4039* (F). **Heredia:** E of San Ramón, *Loiselle 106* (MO); Porto Viejo-Río Sucio, *Croat 35753* (F, MO, PMA); La Selva, Puerto Viejo de Sarapiquí, *Croat 44317* (MO); La Selva, OTS Field Station on the Río Puerto Viejo just E of its jct. with the Río Sarapiquí, *Hammel 8874* (DUKE, F, MO), *Grayum 2780* (DUKE, F, MO); La Selva, 6 km by rd. from Río Peje crossing, 5 km SSE of Masasay, *Schatz & Grayum 706* (DUKE); Puerto Viejo just E of jct. with Río Sarapiquí, *Folsom 10116* (DUKE); Occidental trail, *Kress 84-1630* (SEL); Río Sucio, near Porto Viejo, *Croat 35682* (MO); Zona Protectora, N slopes of Volcán Barba, betw. Río Peje and Río Guacimo, *Grayum & Schatz 3174* (DUKE). **Limón:** along hwy. 32 from Turrialba to Limón, ca. 11 mi. S of Siquirres, *Croat 43333* (ISC, MO, PMA, WISC); Guapiles, *Leon 720* (F); Guapiles, Toro Aurarillo, *Leon 26573* (CR); Finca Anai, at headwaters of Quebrada Mata de Limón, W of Mata de Limón (Sixaola region), *Grayum & Schatz 5279* (CR, MO); Finca Castilla, *Dodge & Goerger 9489* (MO); 7 km SW of BriBri, *L. Gómez et al. 20405* (B, MO); drainage of Río Parismina and Río Reventazón, *Shank & Molina 4288* (DUKE); 10 mi. S of Punta Cahuita, ca. 3 mi. S of turnoff to BriBri, *Croat 43201* (MO); Ref. Barra del Colorado, Río Chirripócito-Río Sardina, *Grayum 9804* (CR, MO); Par. Tortuguero, Est. Biol. Agua Fría, Sendero Las Lomas, 5 km from station, *Robles 1142* (CR, MO); Sendero Los Raudales, 8 km SE from station, *Robles 1158* (CR, MO); PN Tortuguero, Lomas de Sierpe, 4 km NE of station along Río Sierpe, *Robles et al. 2050* (CR, G, MO); Tortuguero Cantón, BriBri-Suretka, *Barringer 3525* (CR, F); Res. Indígena Talamanca, Sukut, mouth of Río Sukut at Río Uren, *Hammel et al. 17548* (CR, MO); Río Reventazón, Finca Montecristo below Cairo, *Standley & Valerio 48997* (US); Río Segundo, Asunción, *L. Gómez & Herrera 23477* (MO); Río Sixaola, BriBri-Caribbean coast, *Baker & Burger 90* (F, MO); Limón-Shiroles, Río Sixaola, 0.9 mi. SW of Bambu, 6.5 mi. SW of BriBri, *Croat 43298* (MO); Río Sixaola, ca. 0.5 mi. SW of Bambu, ca. 3 mi. NE of Bratsi, *Croat 43266* (CR, MO); Tortuguero Cantón, BriBri-Sixaola, NW of Paraiso, *Barringer et al. 3479* (CR, F); Cordillera de Talamanca, headwaters of Quebrada Kakebeta below divide between Río Xikiari and Río Boyei, *Grayum 10858* (CR, INB, MO). **Puntarenas:** Cordillera de Tilarán, Bosque Eterno De Los Niños, Laguna Poco Sol, 18 km ENE of Monteverde, *Haber et al. 10824* (CR, INB). **San José:** Cañón del Río Grande de Orosi, *Chacón et al. 1488* (CR, MO); La Hondura, *Standley 36314* (US); Vázquez de Coronado, Braulio Carrillo NP, along Hwy. San José to Siquirres, along trail to Río Sucio, site of the Old Carillo Station, *Croat 78787* (MO). NICARAGUA. **Río San Juan:** "Los Filos" near Loma Los Filos, Río Santa Cruz, *Salick 8153* (MO). **Zelaya:** ca. 6.3 km S of bridge at Colonia Yolaina and ca. 0.8 km S of ridge of Serranías de Yolaina on rd. to Colonia Manantiales, Colonia Somoza, *Stevens 6420* (MO); Río Punta Gorda, Atlanta, mouth of Caño el Guineo, *Moreno & Sandino 12855* (MO), *Moreno & Sandino 12891* (MO); Río Punta Gorda, Atlanta, Caño Negro mouth of Río Chiquito, *Moreno & Sandino 12917* (MO); Río Punta Gorda, Atlanta, mouth of Caño del Oro at Río Chiquito, *Moreno & Sandino 12955* (MO); Río Punta Gorda, Caño El Guineo, *Tellez et al. 4875* (MEXU, MO). PANAMA. **Bocas del Toro:** Limit trail, Parque Intl. La Amistad, from Quebrada Boca Chica to Quebrada Bonyic, *Polanco 1615* (PMA); 7.7 mi. W of Chiriquí Grande, 1.5 mi. W of Punta Peña, *Croat & Grayum 60112* (CR, MEXU, MO, PMA); Chiriquí Grande-Fortuna, 13.2 mi. W of Chiriquí Grande, *Croat & Grayum 60139* (B, MO, PMA); Fortuna-Chiriquí Grande Hwy. near Cont. Div., 1.1 mi. from main hwy., *Croat & Grayum 60355* (MO); Chiriquí Grande-Fortuna, above waterfall, 1.6 mi. N of Cont. Div., *Croat & Zhu 76450* (CR, MO, PMA, SCZ, US); Changuinola, near Luzon, *Kennedy 3253* (MO); Changuinola-Almirante, Mile 7.5, *Croat & Porter 16249* (MO); Gualaca-Chiriquí Grande, 6.6 mi. N of bridge over Fortuna Lake, *Croat 66732* (MO); Gualaca-Chiriquí Grande, 1.6 mi. N of Cont. Div., *Croat 74930* (MO); Gualaca-Chiriquí Grande, 8.1 mi. S of Punta Peña, *Croat 74952* (MO); N of Fortuna Dam, *McPherson 11129* (MO); rd. to Chiriquí Grande, *McPherson 7371* (MO); 5.3 mi. N of Fortuna Dam, then 1.4 mi. W along gravel rd. to Cont. Div. trail, *Croat & Zhu 76328* (MO, PMA); along Cont. Div. trail, *McPherson 9865* (MO); Fortuna Dam-Chiriquí Grande, 1 mi. from Cont. Div., *Churchill & Churchill 6252* (MO); Río Cricamola, Finca St. Louis-Konkintoë, *Woodson Jr. et al. 1909* (F, MO). **Chiriquí:** Gualaca-Fortuna Dam, 10 mi. NW of Los Planes de Hornito, *Croat 50049* (CR, MO); vic. Fortuna Dam of Río Chiriquí, *Croat 66533* (B, CM, ENCB, DUKE, KYO, L, MO, NY, OOMOTO, QCA, SAR, TEX, US); 4.5–5 km N of Fortuna Lake, *Croat & Grayum 60070* (INB, MO); 7.9 mi. beyond (NW of) Los Planes de Hornito, *Croat 49932* (MO); Gualaca-Bocas del Toro border, km 111, *Gordon 339* (PMA); Fortuna Dam site N of Gualaca, 7.7 mi. beyond Los Planes de Hornito, *Croat 48778* (MO). **Coclé:** vic. El Valle de Antón, La Mesa, Finca Macarenita, *Croat & Zhu 76653* (BM, C, FSU, GOET, INPA, ITIC, L, LE, MO, QCA, PMA, R, TEFH, UB). **Darién:** Mamey, *Whitefoord & Eddy 372* (BM, MO, PMA). **San Blas:** Río Armila, 10 km WSW of Puerto Obaldía, *Mori et al. 6814* (MO). **Veraguas:** valley of Río Dos Bocas, 11 km from Escuela Agrícola Alto Piedra (above Santa Fe) on rd. to Calovebora, *Croat 27490* (MO); NW of Santa Fe, 11 km from Escuela Agrícola Alto de Piedra, in valley of Río Dos Bocas, *Mori et al. 3817* (F, MO); 0.6 mi. beyond Escuela Agricola Alto Piedra, *Croat & Folsom 33989* (MO); 1.7 mi. past Alto Piedra School, *Croat & Zhu 76858* (MO, PMA); beyond Escuela Agrícola Alto Piedra, *Croat 49070* (MO); 3–5 mi. N of Santa Fe, *Gentry 3035* (MO); vic. Escuela Agricultura Alto Piedra near, *Antonio 2994* (MO); 0.6 mi. beyond Escuela Agrícola Alto Piedra, *Croat & Folsom 34042* (MO); Cerro Tute reserve, along ridge to summit, *Croat 66993* (HUA, MO,

PMA); trail to top of Cerro Tute, *Croat 48903* (MO, PMA); Cerro Tute, *Sytsma & Antonio 3006* (MO). COLOMBIA. **Antioquia:** Murrí, La Blanquita, Río Murrí, Transect 7, *Gentry et al. 75903* (MO); Villa Arteaga, *Gutierrez, G. & Barkley 17115* (COL); PN Natural "Las Orquideas," Venados arriba, Río Venados, *A. Cogollo et al. 3462* (JAUM, MO); Mutatá, Río Chontadural, Hacienda El Darién, *Fonnegra 1344* (HUA); Carepa, Est. Exp. de Tulenapa (CA), *Callejas et al. 9704* (NY). **Chocó:** Serranía de Baudo, Las Animas-Pato, Río Pato, ca. 4 km SW of Pato, *Croat 56112* (CHOCO, JAUM, K, MO); Medellín-Quibdó, km 208.5, 9 km W of Tutunedo, ca. 9 km E of Quibdó, *Croat 56205* (CHOCO, COL, CUVC, HUA, MO); Quibdó-Medellín, km 185, 14 km E of Tutunendo, *Croat 56282* (CHOCO, COL, JAUM, MO, PMA); San José del Palmar-Novita, vic. Santa Rosa, *Croat 56625* (COL, HUA, MO); Quibdó-Medellín, 25 mi. E of Quibdó, *Croat 52300* (F, MO, PMA); ca. 2 km E of Playa de Oro, *Croat 57427* (CHOCO, MO); Pueblo Rico (Risaralda)-Istmina (Chocó), Quebrada Antón, 15 km W of Santa Cecilia, 6 km W of Chocó-Risaralda border, *Croat 70900* (MO); Medellín-Quibdó, 85 km W of Bolívar, *Croat 49310* (MO); Acandí-Serranía del Darién, *Juncosa 619* (MO); Pueblo Rico (Risaralda)-Istmina (Chocó), 1 km W of Guarato and Río Guarato at Risaralda and Chocó border, *Croat 70868* (CM, MO); Nuquí, Quebrada Chaquí, *Galeano 4600* (MO); Arusí, El Amargal, trail to Arusí, *Mora 51* (COL), *Croat & Mora 83696* (MO); Quibdó, Tutunendo-Alto del Viente Rd., 25 km N of Quibdó, *Callejas & Jangoux 2692* (HUA). **Nariño:** Río Timbiquí, *Lehmann 8876* (K); valley of Río Imbi, Pasto-Tumaco, vic. "Palmar" 3 km NW of Ricaurte, ca. 1 km E of Texas Gulf Pipeline Maintenance Station, Río Imbi, *Croat 71461* (MO). **Risaralda:** Pueblo Rico, Santa Cecilia, Quebrada La Calera, *Betancur et al. 3054* (MO). **Valle del Cauca:** Cali-Buenaventura, Loboguerrero-Cisneros, Quebrada la Guinea at 1.2 km E of Cisneros, *Croat 62831* (COL, HUA, MO, UB); vic. Queremal, Río Cava, *Croat & Gaskin 80391* (CUVC, MO); Cordillera Occidental, Río Digua, *Cuatrecasas 15053* (US); Bajo Calima, Buenaventura-Malaga, km 51.3, *Croat 71017* (MO); Buenaventura-Málaga, Pulpapel facilities at km 9, *Croat 70099* (MO). ECUADOR. **Esmeraldas:** San Lorenzo, Río Palavi, vic. AWA encampment, *Hoover et al. 3161* (MO); Awá camp to Río Palaví, *Hoover et al. 3968* (MO); Lita-San Lorenzo rd., 14.2 km W of Río Lita Bridge (below Lita), *Croat et al. 82305* (MO); 17.3 km E of Río Tululbí, *Croat 83126* (MO, WU); 33.0 km E of Gasolinera San Lorenzo, Río San José, 1.1 km N Lita-San Lorenzo rd, *Croat 83889* (AAU, F, GB, MO, NY, QCA, S); Lita-San Lorenzo Rd., 1.2 km W of El Durango, 21.1 km W of Alto Tambo, *Croat et al. 82441* (MO, QCNE); Lita-Carondelet Rd., km 16, *Schwerdtfeger 21422* (MO); Bilsa Biol. Res., Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabela, *Pitman & Bass 995* (MO, QCNE); Fila de Bilsa, 7 km E of San José de Bilsa, ca. 80 km due SW of Esmeraldas, 12 km SE of El Salto on Atacames-Muisne Rd., *Gentry et al. 72955* (MO); Eloy Alfaro, comuna de Corriente Grande (Río Chimbagal, tributary del Cayapas), *Yanez et al. 1387* (MO); Res. Ecol. Cotacachi-Cayapas, Charco Vicente, Río San Miguel, *Palacios & Tirado 11287* (MO, QCNE); Quininde, Herrera-Los Monos, headwaters of Río Aguacatal, *Palacios 13626* (CM, MO, QCNE, US); NE of Las Golondrinas, Sitio La Bella Jungla, Cooperativa Unidos Venceremos, *Palacios 11452* (MO, QCNE). **Loja:** Río Pichimá, *Forero 719* (COL, MO). **Pichincha:** Río Palenque Science Center, halfway between Quevedo and Santo Dominga de los Colorados, *Gentry et al. 24700* (MO); rd. E of Santo Domingo-Quevedo rd. (beginning 10.5 km N of Patricia Pilar), Caserío Palmar de Bimbe, *Croat 57000* (CM, MO); Centinela, 12 km E of Patricia Pilar on border with Los Ríos, *Gentry 26705* (MO); Centinela, Montañas de Ila, 13 km E of Patricia Pilar, ca. 54 km S of Santo Domingo, *Hammel & Trainer 15836* (MO).

26. Dieffenbachia wendlandii Schott, Oesterr. Bot. Z. 8: 179. 1858. TYPE: El Salvador. Santa Ana, *H. Wendland s.n.* (holotype, GOET!). Figures 26, 28B.

Stout herb, to (0.8)1.2–2(3) m tall; sap strong and foul-scented (only weakly foul-scented in some Atlantic slope populations); stems erect, decumbent at base; *internodes* dark green to blackish green or medium green, glossy to semiglossy, 1–5 cm long, 2–5.2 cm diam.; *petioles* (11.5)16–32(65) cm long (averaging 25 cm long), matte, medium dark green, sometimes finely darker green-striped throughout (or at least near the base), often weakly glossy toward the apex, moderately spongy, obtusely and shallowly sulcate (sometimes more acutely sulcate near the apex) to D-shaped, sometimes with a slender erect margin or often terete in populations in eastern Mexico, sheathed (0.3)0.5–0.9 their length; sheath (6)12–30(45) cm long (averaging 18 cm long); sheath sometimes markedly undulate on that portion clasping stem, incurled throughout its length with the margins incurled to erect and touching or well-spaced, initially decurrent or nearly so at the apex and with one side completely hiding the other from above the middle, sometimes with the margins somewhat erect and eventually ± emarginate with one side rounded, the other side rounded and somewhat free-ending, rarely with the apex broadly rounded and free-ending; unsheathed portion of petiole (1)3.5–12(24) cm long (averaging 8 cm long), terete or thicker than broad, 12–14 mm diam., 13–15 mm thick, usually obtusely sulcate except terete in some areas on the Atlantic slope of Mexico (the sulcus sometimes broader toward the apex); *blades* narrowly ovate to ovate-elliptic, (15)20–55(65) cm long, (9)10–22(28) cm wide (averaging 35 × 17 cm), 1.3–2.4 times longer than broad (averaging 2 times longer than broad), subcoriaceous to moderately coriaceous, acute and apiculate to abruptly or gradually acuminate at apex (sometimes rounded and apiculate), acute to obtuse or rounded and attenuate at base, sometimes rounded to subcordate, slightly inequilateral, one side 0.8–3.0(4.5) cm narrower than the other; upper surface dark green, semiglossy to weakly glossy, drying gray-green to yellow-brown; lower surface paler, matte or nearly so, drying yellow-green to yellow-brown (both surfaces dark yellow-brown on very old specimens); *midrib* flat to broadly sunken

Figure 26. *Dieffenbachia wendlandii.* —A. Habit, plant with open inflorescence. —B. Adaxial blade surface. —C. Potted flowering plant with open inflorescence (*Croat 39749*). —D. Open inflorescence at anthesis (*Croat 47219*). —E. Staminate portion of spadix and spathe blade. —F. Close-up of spathe showing part of pistillate portion, the mostly sterile portion and the base of the staminate portion. A, B. (*Croat 47219*); D, E, F. (*Croat 47219*).



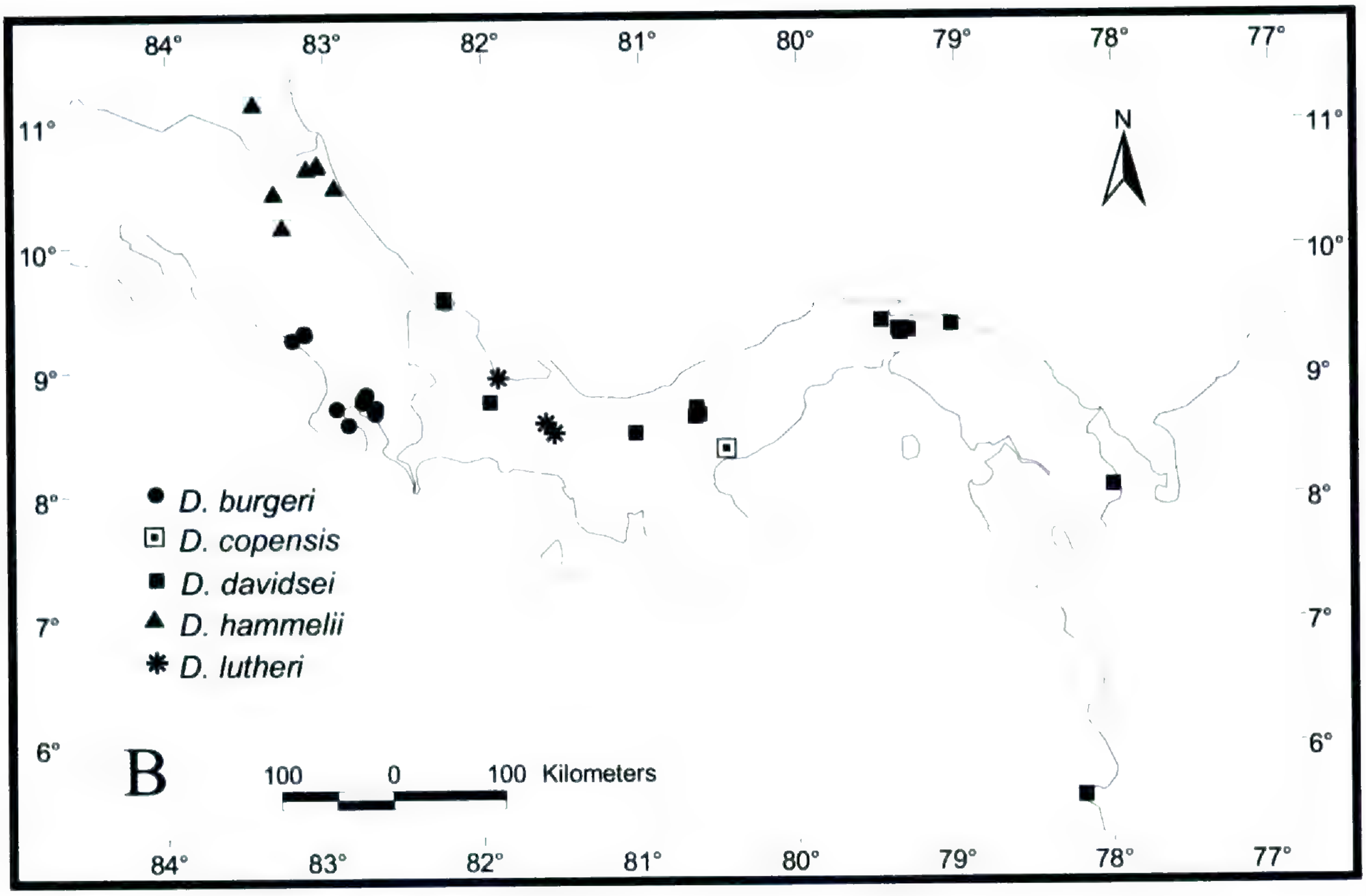
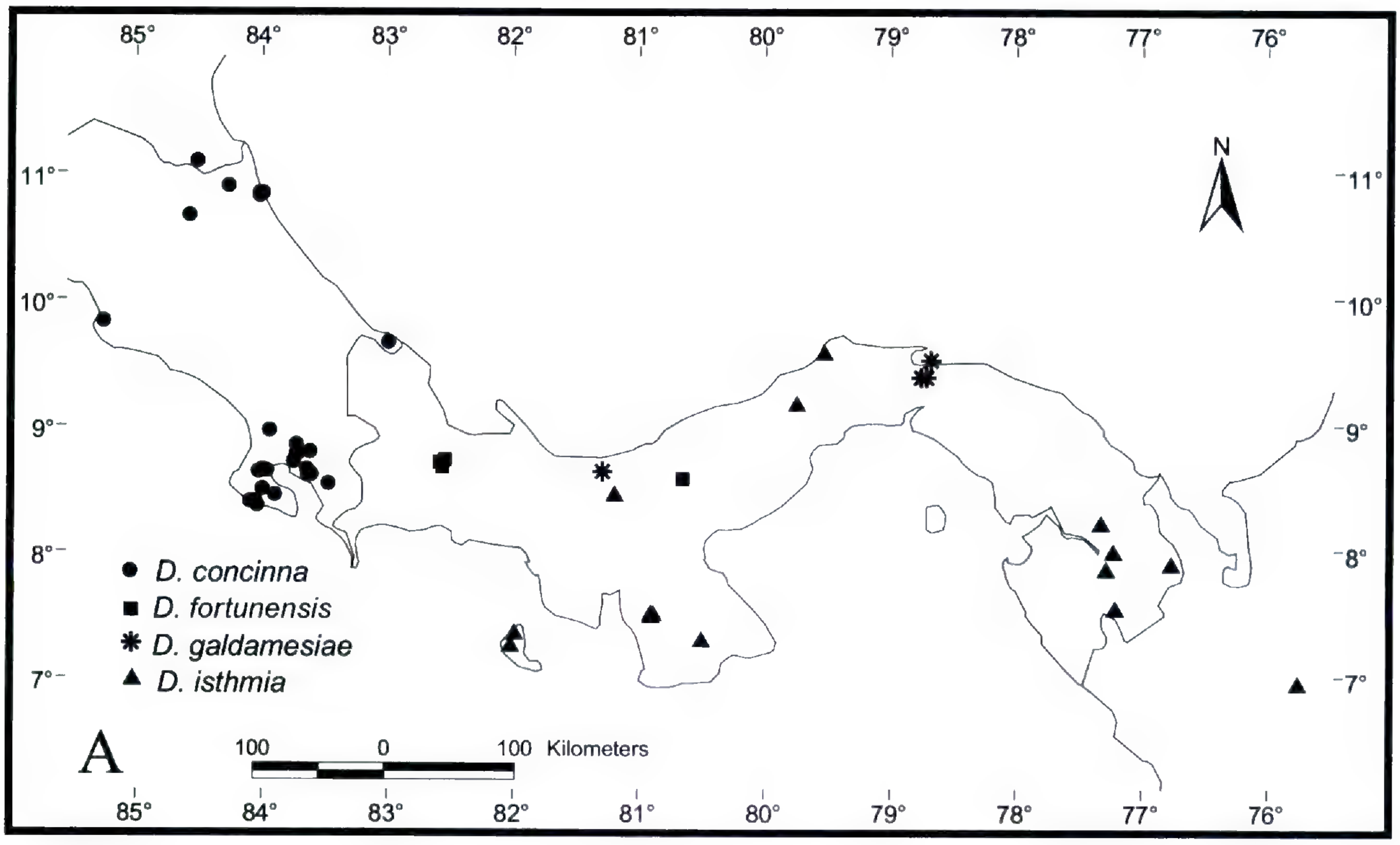


Figure 27. Distribution map. —A. *Dieffenbachia aurantiaca, D. crebripistillata, D. fosteri, D. grayumiana,* and *D. horichii.* —B. *Dieffenbachia burgeri, D. copensis, D. davidsei, D. hammelii,* and *D. lutheri.*



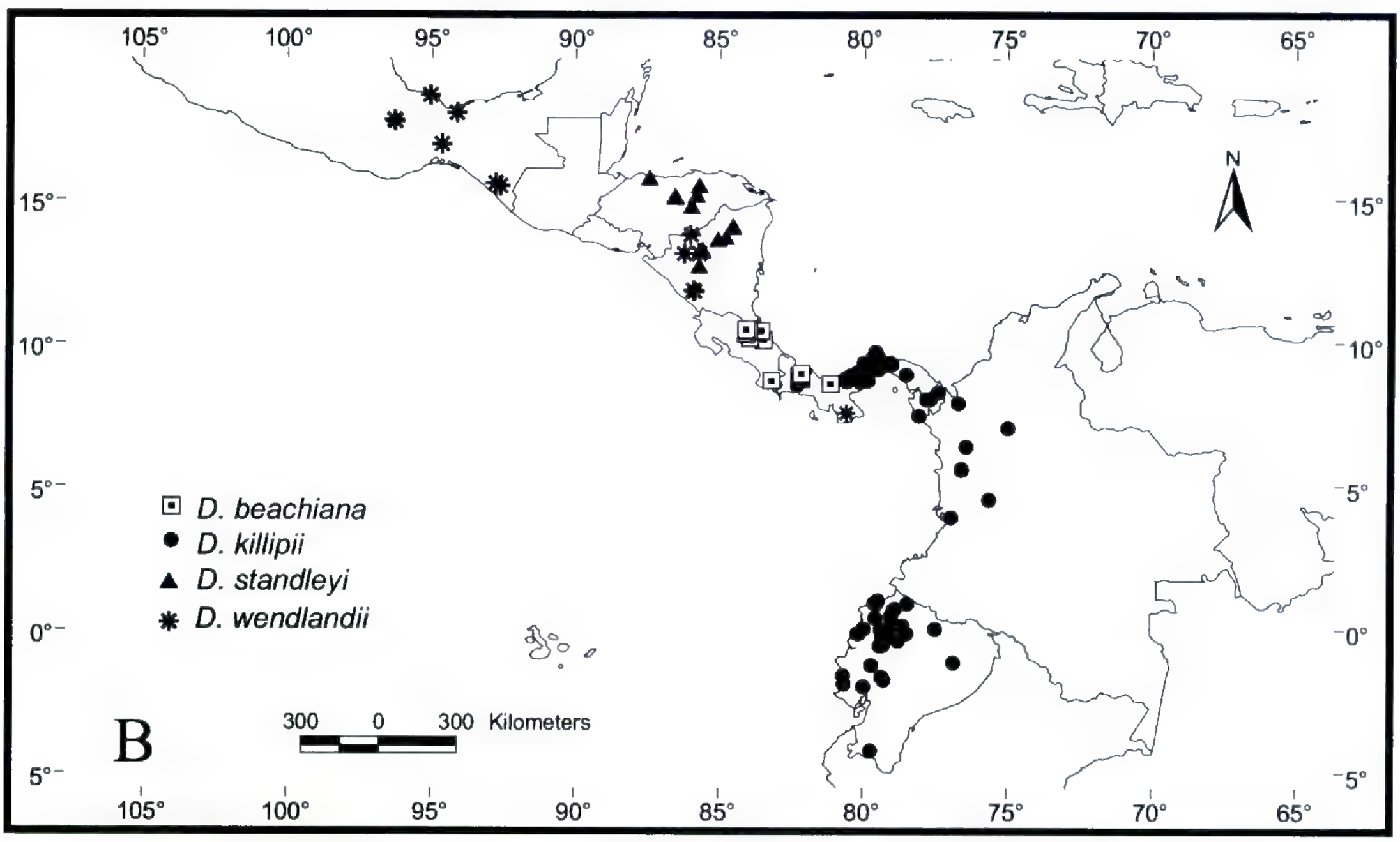
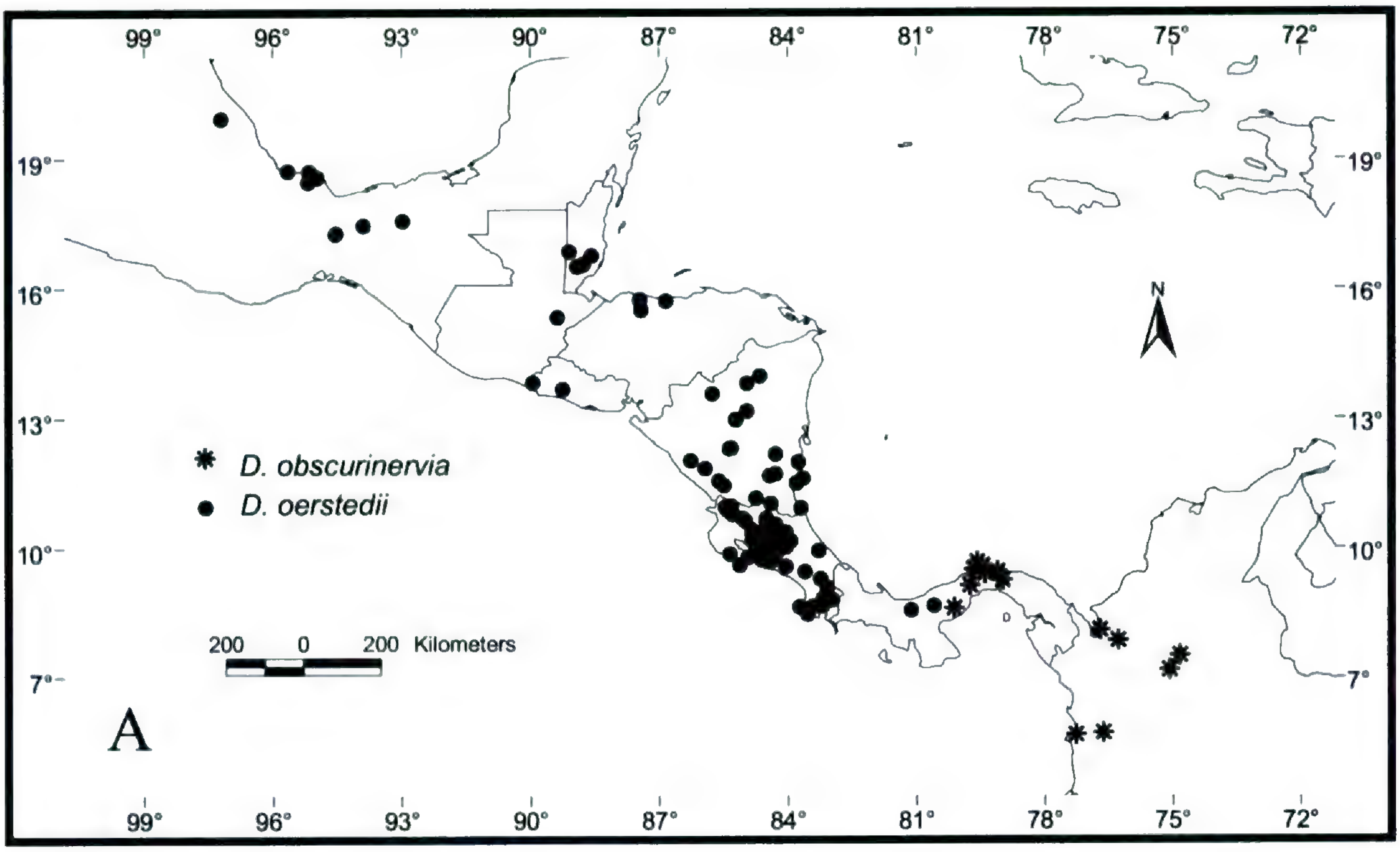


Figure 28. Distribution map. —A. *Dieffenbachia concinna, D. fortunensis, D. galdamesiae,* and *D. isthmia.* —B. *Dieffenbachia beachiana, D. killipii, D. standleyi,* and *D. wendlandii.*

to flattened and concolorous to weakly paler above with fine, close, slightly paler striations, convex to round-raised or narrowly rounded and slightly to moderately paler beneath, usually faintly striate, drying somewhat orange-tinged and paler than the surface, 5–10(18) mm wide; *primary lateral veins* (6)7 to 11(13) per side, weakly and obtusely quilted-sunken above, convex, weakly pleated-raised beneath, arising at an acute angle then spreading at (40°)55°–70° angle, slightly paler than surface



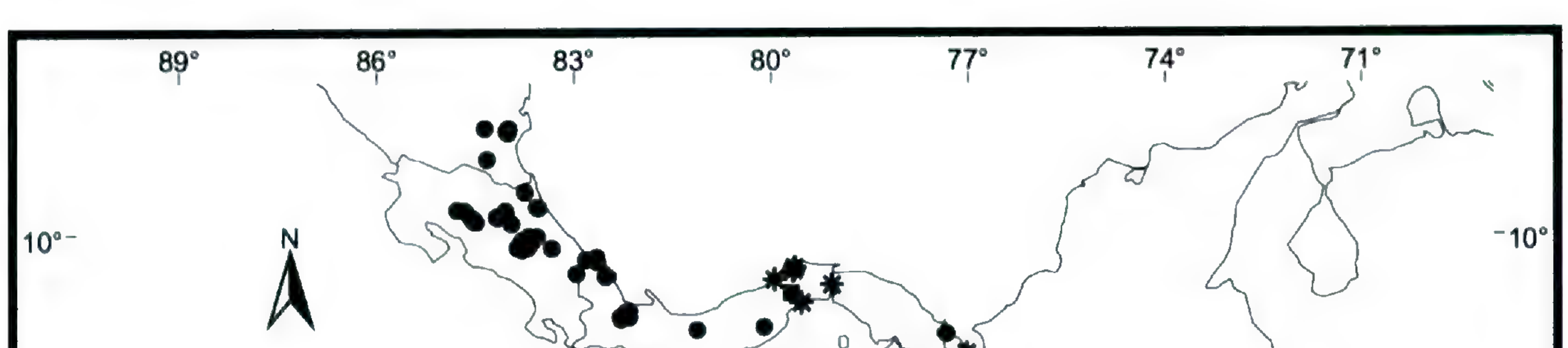
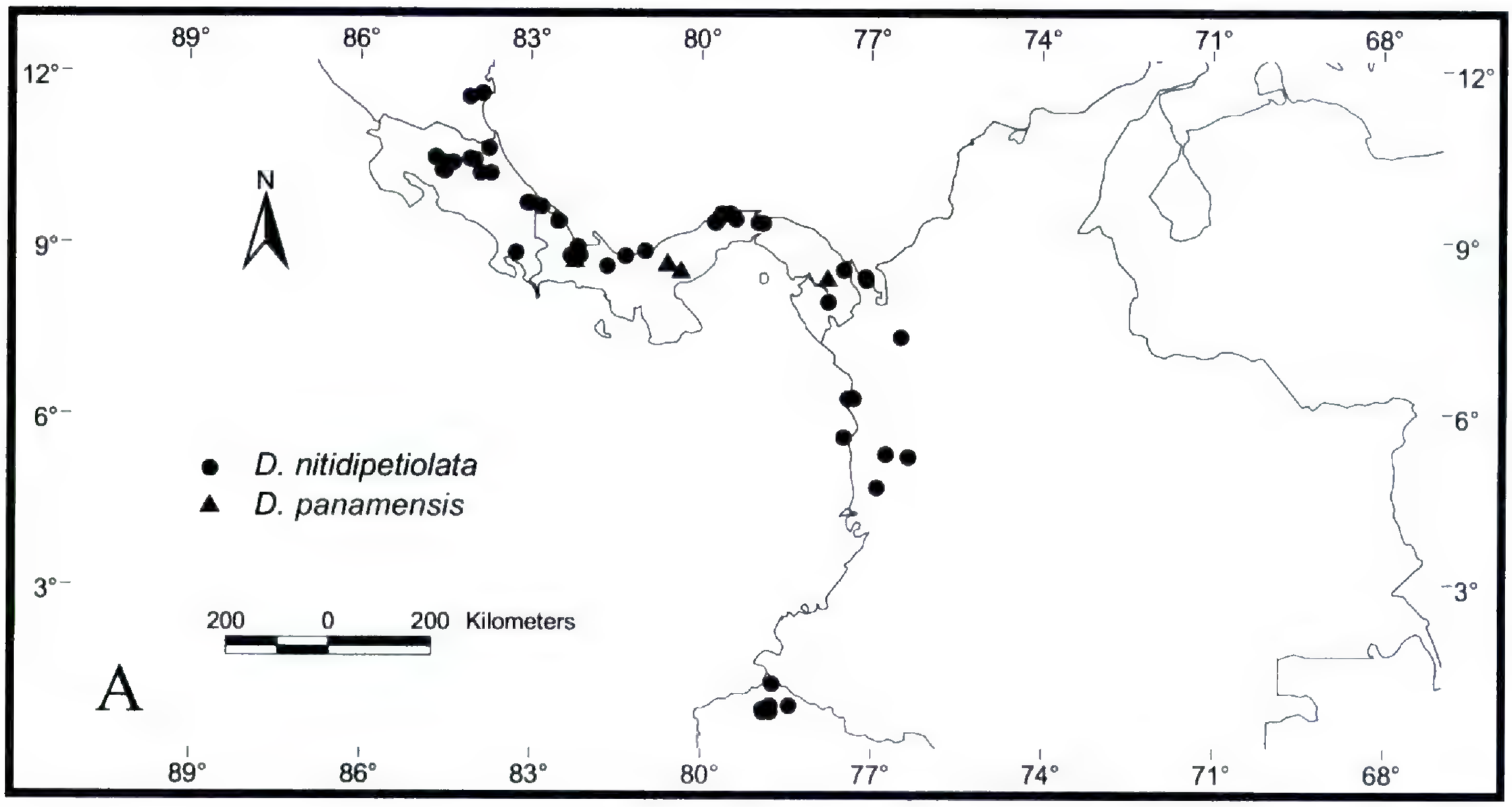


Figure 29. Distribution map. —A. *Dieffenbachia obscurinervia* and *D. oerstedii*. —B. *Dieffenbachia longispatha*, *D. pittieri*, and *D. tonduzii*.

when fresh, usually drying darker than surface, sometimes lighter than surface, moderately straight or weakly curved to near the margin then gradually curved upward along the margin to form a series of closely parallel marginal veins that do not form a collective; minor veins on lower surface moderately obscure on fresh material, more prominent and darker than surface on drying. INFLORESCENCE



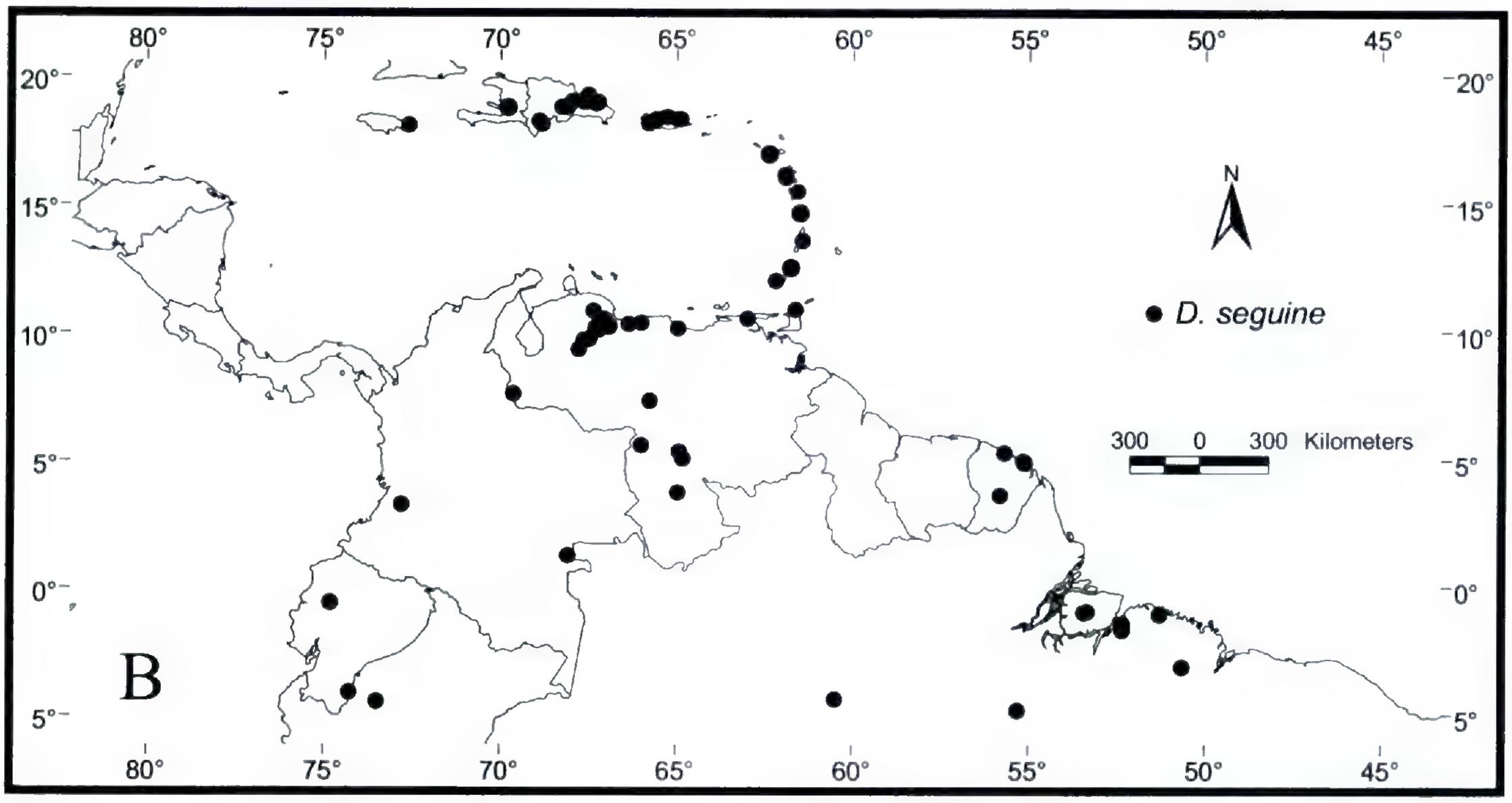


Figure 30. Distribution map. —A. *Dieffenbachia nitidipetiolata* and *D. panamensis*. —B. *Dieffenbachia seguine*.

1 to 4 per axil; bracteoles to 25 cm long; *peduncle* (7)12–22 cm long, 1–1.5 cm × 0.8–1.3 cm diam., subterete, pale medium green, weakly glossy, faintly and finely striate-streaked; *spathe* (16)25–32 cm long, narrowly acuminate to cuspidate-acuminate at apex (the tip turned back), medium-green, weakly glossy to semiglossy outside, equally colored and glossy within with weak, darker, short oblique lines running between the parallel vertical veins throughout the length of the spathe; the spathe tube 8–12 cm long, (2.7)3.5–4.5 cm diam. when furled, 6.5–12.5 cm wide when flattened, with dense minute depressions scattered throughout the tube; constricted portion of spathe (2)3.3–4.0 cm wide, 3.5–8 cm wide when flattened; spathe blade 3.7–4.5 cm wide, flattening to 3.3–6.3 cm wide; *spadix* (12)18–29.3 cm long, 2.0–4.7 cm shorter than the spathe, scarcely protruded forward, its stipe 1–2 cm long, 1.3 cm diam.; the free portion of the spadix 9–11 cm long; pistillate portion (5.5)8.5–10 cm

long, 1.2–1.7 cm diam., 0.9–1.1 cm on drying (rachis 0.9–1.2 cm diam.), the upper 1 cm sometimes with as few as two apparently fertile flowers; staminate portion of spadix (7)9–16 cm long, the fertile staminate portion (4.5)7–12.5 cm long, gradually tapered toward both ends, (0.7)1–1.3 cm diam. midway, 7 mm diam. 1 cm below the apex; mostly sterile intermediate portion of spadix 2.0–4.0 cm long, 7–9 mm diam., with a few aborted pistillate flowers in the lower half and a few sterile male flowers in the apical half, often with a totally barren segment of up to 1–2.8 cm long; pistils (33)45 to 55, depressed-globose, weakly pale yellow-green, moderately glossy, (2)3 to 5 across the width of the spadix, 3.0–3.7 mm diam., 1.5–1.7 mm high; stigma yellow to pale orange, 0.6–1 mm high, 2.0–2.7 mm diam., sometimes broadly sunken medially, sometimes with a prominent, protruding dome held slightly above the outer ring; staminodia 3 to 4, free to the base, broadened toward the base, 0.8–1.2 mm wide at base and sometimes partly fused, usually slightly thicker near apex, (2.5)3.5–5 mm long, white, slightly flattened, 1.5–3.5 mm wide, about as long as the pistils; synandria 4 to 7 visible per spiral, 3.5–4.0 mm diam., widely spaced at base, truncate and smooth at apex, irregularly rounded, pale tan, becoming bowl-shaped and brown except for white, erect margins, margins sometimes crenate, with thecae 6 to 8 per synandrium, these subglobose, ca. 1 mm long, held just below the apex of the synandrium. INFRUCTESCENCE with spathe green at maturity; *berries* red to bright orange, 6–8 mm diam.

Distribution and habitat. *Dieffenbachia wendlandii* occurs principally in seasonally dry habitats on the Pacific slope of Central America, ranging from central Mexico (Oaxaca and Chiapas) to Guatemala (Escuintla, Huehuetenango, San Marcos, Suchitepéquez), El Salvador, Honduras (Morazán), Nicaragua (Estelí, Granada, Matagalpa, Nueva Segovia, Zelaya), Costa Rica (Puntarenas Province), and Panama (Veraguas) at elevations of 75 to 900 m. In Mexico the species occurs on the Atlantic slope only in the State of Oaxaca in the Serranía de Juárez at 250–705 m and in Veracruz in or near the Estación Biológica de Los Tuxtlas near the Caribbean coast at 5–165 m elevation. The only collection of the species in Panama, from Bahía Honda in Veraguas Province, is unusual in having blades more ovate and in drying pale green. It may prove to be a new species.

Phenology. *Dieffenbachia wendlandii* flowers principally in the rainy season, beginning in May and especially in June and July, but continuing until August or rarely September. What appears to be a secondary flowering period may occur in the early dry season because flowering collections have been seen in December and February. Most fruiting specimens have been made in the dry season and early wet season from January to May.

Discussion. The species is characterized by its robust, but moderately short stature, dark green, semiglossy stems; narrowly ovate to ovate-elliptic yellowish brown, to yellow-green-drying leaf blades; but especially by the partially sheathed petioles with the sheath margins decurrent or ending abruptly and rounded at apex with a free, unsheathed sulcate portion 1–9 cm long at the apex. In addition, the species has an unusually large spathe for the size of its leaves, frequently exceeding 30 cm long.

Populations of *D. wendlandii* on the Atlantic slope have petioles completely terete, rather than sulcate adaxially, but this varies even on the same individual. In addition, these populations are more likely to have the petiole sheath even more decidedly decurrent at the apex. At least the populations of plants in Oaxaca at middle elevation above Valle Nacional have sap that is only mildly odorous, whereas elsewhere the sap is malodorous, smelling somewhat like skunk or peccary.

Dieffenbachia wendlandii is easily confused with *D. oerstedii* on the eastern slopes of Chiapas and Veracruz, but *D. wendlandii* is much more robust than plants of *D. oerstedii*, which are usually less than 1 m tall and have internodes usually less than 2.5 cm in diameter. In contrast, the stems of *D. wendlandii* are rarely less than 2.5 cm in diameter and are usually 4–5 cm in diameter. Other differences in *D. oerstedii* are the sharply sulcate (rather than terete to obtusely sulcate) petioles that are white (rather than green) at the base, and the sheath apex of which at least one margin is rounded and prominently free-ending. In contrast, *D. wendlandii* on the Atlantic slope is more than 1.5 m tall at maturity, has internodes more than 3 cm in diameter, and petiole sheath margins acute to only weakly protruded at apex with the free portion of the petiole at most obtusely sulcate. Another way *D. wendlandii* differs from *D. oerstedii* is by its typically larger spathe, over 25 cm long versus less than 20 cm long for *D. oerstedii*.

Previously most material of *D. wendlandii* from Mexico and Guatemala has been mistakenly called *D. oerstedii*, and indeed herbarium material without good field notes is difficult to separate. Several of the collections of *D. oerstedii* made in lowland Veracruz (*Holstein & Armbruster 20425*; *Nee 23773*, *29752*, and *29993*) appear to have the petiole

sheath somewhat decurrent without a conspicuous free-ending apex. They are described as plants no more than 1 m tall. It is possible that these represent hybrid plants since both *D. wendlandii* and *D. oerstedii* occur in lowland Veracruz.

Dieffenbachia wendlandii has been confused with *D. standleyi* in eastern Nicaragua. However, that species occurs only on the Atlantic slope and has petioles sheathed completely to the apex and a proportionately longer blade, ranging from 1.9 to 3.5 times longer than wide, and averaging 2.5 times longer than wide. In contrast, *D. wendlandii* has blades ranging from 1.3 to 2.4 times longer than wide and averages only 2 times longer than wide. Throughout its range in western Mexico and Central America, *D. wendlandii* is variable in the blade shape with the proportionately broader blades occurring in Mexico and Guatemala, where they average 1.8 times longer than wide. The collections from El Salvador and Nicaragua, on the other hand, have leaf blades averaging 2.3 times longer than wide. The populations in Mexico and Guatemala have shorter petioles (averaging 19.8 cm long and 22.6 cm long, respectively) than those in El Salvador and Nicaragua (averaging almost 30 cm long).

The single Costa Rican collection made in Puntarenas Province, along the dry road approaching the Monteverde reserve, is noteworthy in being so far out of the range of the species. *Dieffenbachia wendlandii* may have been more widespread in Costa Rica, but much of the drier forests in the country have been eliminated between the Monteverde site and the Nicaraguan border.

Stevens 6027 from Matagalpa Department, Nicaragua, at 510 m is unusual in having the apex of the petiole sheath broad and conspicuously rounded and somewhat free-ending. It may ultimately prove to be a different species.

While many specimens of *D. wendlandii* in Mexico and Guatemala have blades that are subcordate at the base, most collections in El Salvador and Nicaragua have leaf bases attenuate at the base.

Engler (1915), in his revision of Philodendroideae–Dieffenbachieae, considered *D. wendlandii* a synonym of *Dieffenbachia seguine* var. *viridis* Engl., one of many varieties of what he considered a polymorphic species ranging throughout Central America, the West Indies, and South America. In my opinion, Engler misinterpreted the Central American material, much the same as later botanists, including myself, did for years. However, after actually seeing the live plants in the field in both Central America and in the West Indies, there is no doubt that *D. seguine* does not occur in Central America. The material previously determined as *D. seguine* in Central America has proven to be either *D. oerstedii* with blades larger than normal, or *D. wendlandii*.

Additional specimens examined. COSTA RICA. **Alajuela:** Río Cacao, near Atenas, *L. Gómez 19572* (MO). **Puntarenas:** rd. to Monteverde, *Wilbur et al. 15861* (DUKE). EL SALVADOR. *Wendland 410* (GOET); San Salvador, *Calderon 914* (US), *Renson 266* (NY, US). GUATEMALA. **Escuintla:** *Engler 2389* (GH); Escuintla-Alotenango, mi. 6, *Croat 42050* (DUKE, MO); Cucunya at San André Osuna, *Seler 2389* (G), *Seler 2398* (GH). **Huehuetenango:** Cerro Victoria, Finca San Rafael, Sierra de los Cuchumatanes, *Steyermark 49637* (F). **San Marcos:** Finca Armenia near La Trinidad above San Rafael, *Croat 40790* (ENCB, MO); Río Ixpal, below Rodeo, *Standley 68724* (F); Santa Rosa, Chiquimulilla-El Ahumado, N of Los Cerritos, *Standley 79561* (F); E of Cuilapa, *Standley 78161* (F). **Suchitepéquez:** Mazatenango, *Morales 1047* (F, CR); vic. Tiquisate, *Steyermark 47684* (F, MO). HONDURAS. **Francisco Morazán:** San António de Oriente, above El Jicarito, *Standley 21077* (F). MEXICO. **Chiapas:** Escuintla-Monte Ovando, 2.8 km NW of Turquiz, *Croat 47510* (MO); Escuintla-El Triunfo, ca. 1 mi. N of Escuintla, *Croat 43813* (MO); Tapachula-Nueva Aleman, mi. 4, *Croat 43791* (CHIP, CM, MO); Mapastepec, Sierra de Soconusco, *Croat & D. Hannon 63340* (MO); Tapachula-Union Juarez, at km 13.5, 1.3 mi. N of Trinidad, *Croat 47219* (CHIP, MEXU, MO); Acacoyagua, Ejida Las Golandrinas, Cerro Mt. Ovando Trail, *Croat 78480* (MO); Acapetagua, *R. Hernández 473* (MEXU, MO, NY); Escuintla, Esperanza, *Matuda 16765* (F, MEXU); Esperanza, *Matuda 16369* (MEXU). **Oaxaca:** Tuxtepec, 6 mi. W of Valle Nac. on Hwy. 175, *Croat 39749* (AAU, MEXU, MO, RSA, SEL, TEX, UB, US, VEN), *Croat 43931* (MEXU, MO), *Croat & D. Hannon 65536* (MEXU, MO), *Croat 78711* (MO), *Croat 78720* (MO); Sta. Maria Chimalpa, *Hernández 1318* (MO); Arroyo Sangre, ca. 1–2 km al E de Sta. Maria, *Hernández 2586* (MO). **Queretaro:** Huimilpan, Mpio. Comaltepec, Puerto Eligio, *Lopez Garcia & Martin 122* (MO, CR). **Veracruz:** 9.3 mi. from Tabasco/Veracruz border on Hwy. 180 to Coatzacoacos, *Thompson 441*(MO); San Andres Tuxtla, Catemaco-Montepio, 22.2 km N of Catemaco, vic. Est. Biol. Los Tuxtlas, *Croat & M. Pérez 78686* (MEXU, MO), *G. E. Martínez 2287* (F, MEXU, NY); Catemaco, Sontecomapan, arroyo Basuras, *R. Hernández 645* (F, MEXU, NY, US). NICARAGUA. **Estelí:** Estelí-La Concordia, km 14, Río Isiquií, *Moreno 15290* (MO). **Granada:** Volcán Mombacho, Finca Cutirre, *Atwood A212* (MO); Sardela Hacienda Cutirre, *Moreno 16421* (MO); 2 km al SE de la Hacienda Cutirre, *Moreno 16464* (MO), *Sandino 1248* (MO); 1 km SE of Cutirre, *Moreno & Henrich 8427* (MO). **Managua:** *Garnier 772* (US). **Matagalpa:** Hwy. 5 ca. 38.7 km from Hwy. 3 intersection, ca. 5.5 km N of Río Tuma bridge, *Stevens 6027* (DUKE, MEXU, MO). **Nueva Segovia:** ca. 1.6 km W of Murra-El Jícaro, km 1, Quebrada El Carmen, *Stevens et al. 17591* (MO); Río Solonli, Quebrada Tastasli, 3 km S of Jalapa, 6 Apr. 1977, *Neill 1657* (MO). PANAMA. **Veraguas:** Soná, Bahía Honda, 7°58′, 81°17′W, *Ibáñez et al. 1829* (PMA).

Excluded Species

Dieffenbachia lancifolia Linden & André, placed in synonymy of *D. seguine* by Engler (1915); how-

ever, this is a distinct species from Antioquia Department, Colombia.

Dieffenbachia picta Schott forma *lancifolia* (Linden & André) Engl. and *Dieffenbachia picta* Schott subvar. *lancifolia* (Linden & André) Engl. are combinations of *Dieffenbachia lancifolia* Linden & André that also must be excluded from consideration in this revision of Central American *Dieffenbachia*.

Dieffenbachia meleagris Linden & Rodigas, placed in synonymy of *D. seguine* by Engler (1915); however, this is a distinct species from Ecuador, possibly one synonymous with *D. spruceana* Schott. The recombined *Dieffenbachia meleagris* Linden & Rodigas subvar. *meleagris* is also to be excluded.

Dieffenbachia shuttleworthiana Engl. was synonymized with *D. picta* by Engler (1915), but it must be excluded along with the combination *D. picta* Schott forma *schuttleworthiana* (Regel) Engl. and *D. shuttleworthiana* Hort. Bull. This Colombian species is not closely related to *D. seguine*.

Species Incertae Sedis

The following species names are believed to be synonyms of *Dieffenbachia seguine* based on the revision of *Dieffenbachia* by Engler (1915); however, owing to the destruction of many herbarium specimens during World War II, lectotypification was impossible. The specimens were no doubt available during Engler's time, and it is assumed that he saw the material.

Dieffenbachia picta fo. *mirabilis* Engl., Fl. Bras. 3(2): 176. 1878. TYPE: based on a plant of unknown origin cultivated by Verschaffelt, not designated. No type listed by Engler.

Dieffenbachia seguine fo. *decora* Engl., Fl. Bras. 3(2): 175. 1878. *Dieffenbachia seguine* subvar. *decora* (Engl.) Engl., Bot. Jahrb. Syst. 26: 568. 1899. *Dieffenbachia seguine* var. *decora* (Engl.) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 47. 1915. *Dieffenbachia seguine* fo. *decora* (Engl.) Engl., Pflanzenr. IV, 23 Dc(Heft 64): 48. 1915, nom. superfl. *Dieffenbachia decora* Hort. Versch. ex Engl., in DC., Monogr. Phan. 2: 446. 1878. TYPE: based on a plant of unknown origin cultivated by Verschaffelt, not designated. No type listed by Engler.

Dieffenbachia seguine fo. *nobilis* Engl., Fl. Bras. 3(2): 174. 1878. *Dieffenbachia seguine* subvar. nobilis, Bot. Jahrb. Syst. 26: 568. 1899. *Dieffenbachia seguine* var. *nobilis* (Engl.) Engl., Pflanzenr. IV 23 Dc(Heft 64): 47. 1915. TYPE: Brazil. Pará: Barraquin based on a cultivated plant by Verschaffelt. No type listed by Engler.

Dieffenbachia picta subvar. *angustifolia* Engl., Bot. Jahrb. Syst. 26: 569. 1899. TYPE: based on a cultivated plant of unknown origin, not seen. No type listed by Engler.

Dieffenbachia seguine var. *minor* Engl., Bot. Jahrb. Syst. 26: 567. 1899. TYPE: No type listed by Engler.

Dieffenbachia picta var. *latior* Engl., Bot. Jahrb. Syst. 26: 569. 1899. TYPE: No type listed by Engler.

Dieffenbachia picta var. *latior* Engl., Bot. Jahrb. 26. 569. 1899. TYPE: Not seen. No type listed by Engler.

Dieffenbachia picta subvar. *memoria* Engl., Bot. Jahrb. Syst. 26: 570. 1899. TYPE: based on living material at Berlin Botanical Garden (also Buitenzorg), not seen. No type listed by Engler.

Dieffenbachia picta subvar. *mirabilis* Engl., Bot. Jahrb. Syst. 26: 570. 1899. *Dieffenbachia mirabilis* Versch. ex Engl., in DC., Monogr. Phan. 2: 448. 1878. TYPE: based on a cultivated plant of unknown origin by Verschaffelt, not seen. No type listed by Engler.

Dieffenbachia picta var. *angustior* Engl., Bot. Jahrb. Syst. 26. 569. 1899. TYPE: No type or locality listed, not seen. No type listed by Engler.

Dieffenbachia seguine fo. *viridis* Engl., Fl. Bras. 3(2): 174. 1878. *Dieffenbachia seguine* subvar. *viridis* Engl., Bot. Jahrb. Syst. 26: 567. 1899. *Dieffenbachia seguine* var. *viridis* Engl., Pflanzenr. IV. 23 Dc(Heft 64): 45. 1915. TYPE: Not seen. No type listed by Engler.

Dieffenbachia seguine var. *lineata* (K. Koch & Bouché) forma? *decora* (Engl.) Engl., Pflanzenr. IV. 23 Dc(Heft 64): 48. 1915. *Dieffenbachia seguine* var. *decora* (Engl.) Engl., Pflanzenr. IV. 23 Dc(Heft 64): 47. 1915. TYPE: based on a cultivated plant of unknown origin by Verschaffelt, not seen. No type listed by Engler.

Dieffenbachia picta var. *typica* Engl., Pflanzenr. IV. 23 Dc 50. Fig. 21. 1915. TYPE: cultivated in European gardens. No type listed by Engler.

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Appendix 1

List of species.

1. *Dieffenbachia aurantiaca* Engl.
2. *D. beachiana* Croat & Grayum
3. *D. burgeri* Croat & Grayum
4. *D. concinna* Croat & Grayum
5. *D. copensis* Croat
6. *D. crebripistillata* Croat
7. *D. davidsei* Croat & Grayum
8. *D. fortunensis* Croat
9. *D. fosteri* Croat
10. *D. galdamesiae* Croat
11. *D. grayumiana* Croat
12. *D. hammelii* Croat & Grayum
13. *D. horichii* Croat & Grayum
14. *D. isthmia* Croat
15. *D. killipii* Croat
16. *D. longispatha* Engl. & K. Krause
17. *D. lutheri* Croat
18. *D. nitidipetiolata* Croat
19. *D. obscurinervia* Croat
20. *D. oerstedii* Schott
21. *D. panamensis* Croat
22. *D. pittieri* Engl.
23. *D. seguine* (Jacq.) Schott
24. *D. standleyi* Croat
25. *D. tonduzii* Croat & Grayum
26. *D. wendlandii* Schott

Appendix 2

Index to exsiccatae. Type species in boldface

Acevedo-Rodríguez 4705 (23); Acosta Solís, M. 10896 (15); Aguilar, R. 256 (20), 2195 (4), 2380 (20), 2412 (20), 5204 (20); Aguilar et al. 4302 (20); Akers, M. 78 (18), 78A (11); Allen 5669 (4), 5669A (4), 5972 (1); Allen & Alston 1839 (6); Alvarez, A. & P. Herrera 699 (15); Alverson et al. 283 (19), 376 (15); Anaya 1 (20); André 1202 (23), 457 (15); Antonio 2994 (25), 3039 (6), 3820 (6), 4488 (18), 4546 (14), 4638 (15), 226 (15); Antonio & Hahn 4405 (15), 4406 (15); Aranda et al. 2860 (20); Archer 2215 (19); Aristeguieta 1764 (23); Asplund 15574 (15); Atha & Zanoni 770 (23); Atwood 212 (26); Augo 1693 (23); Aymard & Ortega 3090 (23); Aymard et al. 2714 (23).

Bailey 335 (14); Baker & Burger 90 (25); Balick et al. 1738 (20), 2080 (20), 2359 (23), 2716 (20); Barfod & Skov 60101 (18); Barfod et al. 48154 (18), 48348 (18); Barlow s.n. (20); Barringer 1790B (13), 2416 (18), 2432 (11), 3525 (25); Barringer et al. 1973 (4), 3479 (25), 4039 (25), 4061 (20); Bartlett & Gentry 7423 (15); Bay 278 (15); Beach 1429 (20), 1430 (20), 1431 (20), 1432 (20), 1433 (20), 1434 (20), 1435 (20), 1436 (18), 1439 (18), 1440 (11), 1441 (11), 1448 (2), 1485 (2), 1518 (20); Beard 656 (23); Beck 17103 (23); Beck et al. 295 (23); Bello & Cruz 4284 (20); Bello et al. 42 (20); Benítez de Rojas et al. 4661 (23); Bernal et al. 1158 (19); Betancur et al. 1177 (18), 3054 (25); Beutelspacher s.n. (20); Billiet & Jadin 7359 (23), 7346 (23), 7347 (23), 7357 (23), 7358 (23); Billiet et al. 6257 (23); Blackmore & Chorley 4073 (24); Blackwell et al. 2704 (18); Blum & Tyson 2324 (15); Bogner 965 (23); Bourgeau s.n. (20); Brand & Ascanio 277 (14); Bravo 31 (20); Bravo s.n. (MEXU 30199) (20); Bravo & Nú 107 (20); Breedlove 12752 (20), 24166 (20), 33839 (20), 34977 (20), 40155 (20); Breedlove & McClintock 34192 (20); Breedlove & Thorne 30681 (20); Britton 447 (23), 4126 (23); Britton & Britton 7897 (23), 9664 (23), 10082 (23); Britton & Shafer 1625 (23); Bunting 1692 (23), 2026A (23), 2027 (23), 2035 (23), 2036 (23), 2044 (23), 2622 (23), 2678 (23), 2729 (23), 2738 (23), 2829 (23), 3321 (23), 11687 (23), 13515 (23); Bunting & Fernandez 3295 (23); Bunting & Holmquist 4319 (23); Bunting & Manara 2119 (23), 2120 (23), 2122 (23), 2123 (23), 2124 (23), 2124V (23), 2125 (23), 2126 (23), 2127 (23);

Bunting & Trujillo 2236 (23); Bunting et al. 1937A (23), 1949A (23), 1997 (23), 2072 (23), 2074 (23), 2073 (23), 4108 (23); Burch et al. 1123 (15); Burger & Antonio 10905 (18), 11198 (18), 11224 (12), 11249 (4); Burger & Baker 9968 (11), 10121 (3), 10137 (13); Burger & Gentry Jr. 8898 (3); Burger & Liesner 7111 (20), 7196 (4), 7254 (3); Burger & Matta 4181 (11); Burger & Pohl 7825 (20); Burger & Stolze 5024 (18), 5461 (4), 5489 (3), 5753 (18), 5754 (2); Burger et al. 1323 (20), 10323 (18), 10669 (13), 10671 (3), 10699 (18), 10734 (11), 11695 (20), 11926 (20); Busey 743 (1).

Cadet 6030 (23); Calderon 914 (26); Callejas & Jangoux 2692 (25); Callejas et al. 4873 (19), 5661 (18), 9704 (25); Calzada 338 (20); Camp E-3599 (15), 3653 (15); Carballo et al. 47 (20); Carleton 508 (20); Carlson 153 (20); Carrasquilla 2005 (18); Carrasquilla & Mendoza 1239 (18); Carrasquilla & Rincón 304 (15); Carvajal 273 (20); Catharino et al. 1909 (23); Cedillo, T. 3645 (20); Cerón & J. Corozo 33858 (18), 33947 (18), 34097 (18); Cerón et al. 29159 (15); Chacón 364 (20), 507 (11), 553 (12), 1406 (13); Chacón et al. 1488 (25); Chavarría & Umaña 157 (13); Chavarría et al. 257 (4); Chazaro 416 (20); Chinchilla 137 (20); Churchill & Churchill 6105 (18), 6158 (8), 6159 (8), 6252 (25); Churchill & de Nevers 4333 (15); Churchill et al. 3993 (6), 4032 (15), 4125 (15); Clarke 60 (20); Clewell & Tyson 3306 (15); Clezio 221 (15); Cogollo et al. 3462 (25); Colchester 2108 (23); Conrad & Conrad 2882 (20); Conrad et al. 2863 (20); Cornejo & Bonifaz 3107 (15), 4195 (15), 4828 (15), 5191 (15), 5210 (15); Correa & Montenegro 10419 (6), 10647 (6); Cowan 2063 (20); Cowell 550 (23); Cowgill 532 (23); Cremers 9896 (23); Croat 4095 (16), 4125 (16), 4134 (16), 4576 (14), 5183 (14), 5259 (16), 5317 (14), 5709 (14), 5759 (19), 5761 (16), 5767 (16), 5819 (14), 5896 (14), 6192 (16), 6276 (16), 6308 (14), 6409 (16), 6471 (16), 6502 (14), 6775 (19), 7136 (16), 7455 (16), 7478 (6), 7712 (14), 8623 (19), 10133 (14), 10982 (14), 11291 (14), 11321 (16), 11411 (16), 11420 (6), 11514 (16), 11570 (15), 12086 (6), 12123 (6), 12229 (16), 12319 (16), 12352A (19), 12353 (15), 12401 (15), 12489 (15), 12491 (15), 12660 (19), 13403 (6), 13849 (19), 14175 (6), 14309 (15), 14388 (15), 14504 (15), 14706 (15), 14707 (6), 14789 (6), 15082 (15), 15173 (14), 16769A (18), 16803 (15), 16923 (16), 17210 (6), 17311 (15), 17391A (16), 21412 (23), 21741 (23), 21961 (1), 21999 (20), 22173 (20), 22252 (20), 24250 (20), 25213 (6), 25352 (6), 26193 (6), 26239 (6), 27161 (18), 27196 (16), 27206 (21), 27490 (25), 32955 (1), 33018 (16), 33551 (15), 33568 (6), 34442 (15), 34475 (14), 34654 (16), **34656 (14),** 34745 (14), 35079 (1), 35108 (4), 35206 (20), 35210 (1), 35292 (1), 35682 (25), 35688 (4), 35702 (4), 3575(25), 35915 (6), 35951 (6), 36260 (25), 36297 (20), 36444 (20), 36472 (25), 36473 (20), 36727 (25), 36747 (25), 36821 (25), 36855 (20), 36958 (6), 37268 (17), 37351 (20), 37361 (6), 37383 (15), 37479 (15), 37605 (15), 37746 (18), 38010 (14), 38057 (14), 38120 (18), 38229 (18), 38344 (23), 38669 (15), 38947 (15), 39749 (26), 40062 (20), 40087 (20), 40089 (20), 40107 (20), 40163 (20), 40790 (26), 41855 (20), 42050 (26), 42133 (20), 42556 (24), 42625 (24), 42645 (20), 42676 (24), 43201 (25), 43217 (18), 43298 (25), 43266 (25), 43333 (25), 43368 (18), 43629 (25), 43791 (26), 43813 (26), 43931 (26), 44226 (11), 44246 (20), 44254 (18), 44283 (2), 44307 (18), 44317 (25), 44321 (11), 44558 (6), 44682 (6), 46785 (20), 46945 (25), 46947 (18), 47088 (5), 47219 (26), 47510 (26), 47868 (20), 48437 (15), 48672 (8), 48778 (25), 48816 (15), 48903 (25), 49056 (15), 49070 (25), 49124 (10), 49155 (6), 49243 (6), 49310 (25), 49761 (18), 49768 (18), 49791 (19), 49805 (15), 49932 (25), 49971 (8), 50049 (25), 50480 (15), 50655 (15), 50684 (15), 50725 (15), 52300 (25), 5378 (14), 53921 (23), 53956 (23), 54380 (23), 54649 (23), 55549 (15), 55629 (15), 55666 (15), 56070 (18), 56112 (25), 56205 (25), 56282 (25), 56625 (25), 57000 (25), 57427 (25), 57462 (18), 59152 (2), 60567 (23), 60613 (23), 60867 (23), 62831 (25), 66533 (25), 66732 (25), 66866 (8), 66953 (2), 66993 (25), 67115 (6), 67197 (15), 67329 (19), 67379A (18), 67399A (16), 67480 (15), 67526 (21), 67533 (20), 67576 (6), 67594 (4), 67692 (3), 67700 (1), 67837 (8), 68012 (8), 68069 (20), 68097 (25), 68195 (18), 68196 (25), 68336 (25), 68358 (2), 68359 (11), 68379 (18), 68449 (20), 68494 (23), 68547A (23), 68582 (23), 68679 (15), 68699 (6), **68746 (6),** 68820 (21), 68854 (18), 68961 (15), 68971 (16), 69070 (17), 69343 (15), 70099 (25), 70868 (25), 70900 (25), 71017 (25), 71119 (15), 71461 (25), 72573 (15), 73792 (15), 73826 (15), 74137 (23), 74759 (15), 74760 (6), 74789 (15), 74792 (15), 74853 (20), 74861 (6), 74930 (25), 74945 (11), 74952 (25), 74953 (11), 74958 (18), 75007 (17), 75099 (20), 75100 (7), 75149 (19), 75154 (15), 75172 (6), 75195 (16), 77281 (4), 77283 (20), 77298 (23), 78287 (23), 78318 (4), 78323 (23), 78345 (23), 78480 (26), 78678 (20), 78687 (20), 78695 (20), 78711 (26), 78720 (26), 78731 (12), 78732 (4), 78733 (11), 78758 (12), 78771 (2), 78784 (20), 78787 (25), 78788 (18), 78830 (20), 78838 (25), 78859 (20), 78905 (20), 79072 (20), 79073 (13), 79075 (20), 79076 (4), 79329 (15), 79348 (18), 79359 (15), 82829 (15), 83126 (15), 83889 (25), 87448 (18); **Croat & Alba 1222 (10);** Croat & Bay 75707 (15); Croat & Cogollo 52174 (15); Croat & Folsom 33989 (25), 34042 (25); Croat & Gaskin 80391 (25); Croat & Grayum 59731 (3), 59785 (4), 59814 (3), 59851 (3), 59906 (1), 59929 (20), **60002 (8),** 60070 (25), 60112 (25), 60116 (18), **60130 (2),** 60139 (25), 60149 (11), 60255 (2), 60346 (8), 60355 (25); Croat & D. Hannon 63129 (20), 63167 (20), 63340 (26), 64109 (24), 64317 (24), 64476 (24), 64622 (20), **64638 (24),** 65370 (20), 65536 (26), **74856 (21),** 79112 (3), **79115 (13),** 79167 (4), 79170 (4), **79191 (4),** 79193 (1), 79199 (18), **79211 (3),** 79238 (4), 79284 (20), 79286 (3), 79291 (4); Croat & M. Mora 83652 (18), 83685 (7), 83696 (25), 83777 (16); Croat & Nuñez 82064 (15); Croat & M. Pérez 78686 (26); Croat & Porter 16249 (25), 16303 (18), 16375 (18), 16412 (18), 16499 (11); Croat & Zhu 76203 (16), 76253 (15), 76254 (18), 76256 (16), 76257 (16), 76259 (15), 76266 (16), 76328 (25), 76340 (8), 76422 (18), **76449 (18),** 76482 (18), 76533 (7), 76560 (10), 76597 (7), 76644 (6), 76653 (25), **76666 (15),** 76666A (19), 76746 (15), 76757 (6), 76794 (20), 76858 (25), 76859 (20), 76942 (18), 77017 (7), 77023 (18), 77042 (16), 77048 (15), 77101 (16), 77102 (15), 77115 (14), 77201 (20); Croat et al. 82305 (25), 82441 (25), 82520 (18), 83795 (15), 83804 (15), 84041 (18); Cruz 354 (20); Cuatrecasas 4225 (23), 15053 (25).

D'Arcy 769 (23), 770 (23), 9420 (15), 9678 (6), 10766 (20); D'Arcy & Sytsma 14498 (15); Davidse 35802 (20); Davidse & Brant 31879 (20), 32366 (20), 32410 (20); Davidse & D'Arcy 10098 (15); Davidse & González 13410 (23), 21012 (23); Davidse & Hamilton 23599 (15), 23617 (7); Davidse & Herrera 26262 (20), 31077 (12), 31154 (12), 31213 (11); Davidse & Holland 36505 (20); Davidse & Holst 36041 (20); Davidse et al. 4844 (23), 18102 (23), 20326 (20), 20440 (20), 20914 (23), 29516 (20), 34478 (20), 35484 (24); Davidson 7164 (20); de Nevers & H. Herrera 3975 (7), 5898 (18); de Nevers et al. 4709 (7),

5727 (18), 7407 (18), **7409 (19),** 8267 (15); Delinks 452 (15); Dillon et al. 1837 (20); Dodge 10020 (4), 10198 (4); Dodge & Goerger 9489 (25), 10157 (20); Dodson 6188 (15); Dodson & Dodson 11130 (15); Dodson & Tan 5338 (15); Dodson et al. 8415 (15), 10594 (15), 14638 (15); Donnell Smith 7813 (20); Drake 7 (23); Dressler 4688 (15), 4716 (14), 5316 (10); Dryer 1681 (11); Duke 5014 (14), 5099 (15), 5169 (15), 5260 (15), 5437 (15), 13082 (15), 13601 (15), 14346 (15), 15591 (15); Duke & Kirkbride 14019 (15); Duss, P. 3790 (23), 21496 (23); Dwyer 2077 (15), 4565 (15), 9920 (20), 11184 (20); Dwyer & Dieckman 13008 (20); Dwyer & Gentry 9479 (6).

Eggers 14183 (15), 15095 (15); Ekman 1983 (23); Engler 226 (23), 227 (23), 2389 (26), 2793 (23); Espina et al. 2902 (15); Espinosa & Guerra 3762 (15), 3939 (15); Espinosa & E. Martínez 3308 (6); Espinosa et al. 3138 (15), 3611 (15), 4478 (15), 4723 (6), 10035 (20).

Faden et al. 76/82 (20); Fallen & Ray 860 (15); Fishlock 326 (23); Folsom 1265 (6), 1444 (15), 3211 (6), 4054 (20), 6218 (6), 6247 (15), 8712 (20), 9200 (18), 9329 (12), 9724 (11), 10116 (25); Folsom & Collins 436 (15), 6486 (21); Folsom & Mauseth 7844 (15); Folsom et al. 2111 (20), 6848 (15), 6852 (15), 8264 (21); Fonnegra 1344 (25); Fonnegra et al. 2899 (18), 2907 (18); Forero 719 (25); Forero et al. 1723 (14), 4571 (18), 4659 (18), 6272 (15), 6489 (15), 9007 (15), 9047 (15); Förther 10213 (20); Foster, R. B. 865 (14); **Foster et al. 14649 (9);** Fuentes 367 (20); Fuertes 564 (23); Funk et al. 10626 (25), 10718 (25).

Galdames et al. 1138 (18), 1330 (7), 1570 (7), 1626 (14), 2252 (14), 2286 (14), 2486 (14); Galeano, G. 4600 (25); Galeano, G. et al. 4825 (19); Gamboa et al. 71 (15), 91 (15); Garibaldi 68 (14); Garnier 772 (26); Gentry 3035 (25), 26705 (25); Gentry & Dwyer 3643 (15); Gentry & Forero 7217 (18), 7342 (18); Gentry & Juncosa 41037 (18); Gentry & Lajones 73108 (15); Gentry & Tyson 1653 (14); Gentry et al. 3406 (15), 24700 (25), 26709 (15), 28574 (14), 72496 (15), 72955 (25), 75903 (25); Gómez 19038 (20), 19531 (4), 19532 (20), 19572 (26), 20562A (20), 20565 (20), 22016 (20), 22951 (13); Gómez & Herrera 23477 (25); Gómez et al. 20405 (25), 21108 (20); Gómez-Laurito 7792 (13), 7856 (4); Gómez-Pompa 1505 (20); Gonçalves et al. 224 (23); González 1473 (20), 6711 (20), 3341 (20), 5597 (20); Gordon 55C (18), 339 (25); Grant & Rundell 92–01928 (4); Grayum 2225 (18), 2288 (11), 2771 (20), 2772 (12), 2780 (25), 2840 (4), 4756 (13), 4765 (20), 6194 (20), 6887 (11), 6899 (2), 6918 (20), 6925 (20), 6936 (2), **7620 (12),** 7698 (2), 8638 (13), 9251 (20), 9277 (20), **9773 (11),** 9777 (4), 9804 (25), 9830 (11), 9844 (18), 10588 (4), 10858 (25); Grayum & Evans 10156 (4); Grayum & Fleming 8119 (4); Grayum & Hammel 5785 (18); Grayum & G. Herrera 7829 (20), 9139 (1), 9236 (3); Grayum & Jacobs 3524 (18); Grayum & Murakami 9939 (25); Grayum & Schatz 3174 (25), 3206 (11), 3218 (18), 3220 (2), 5279 (25); Grayum & Sleeper 6100 (20); Grayum & Warner 5710 (20); Grayum et al. 3982 (4), 3983 (4), 4014 (3), 4440 (7), 4447 (4), **4483 (7),** 4961 (20), 5467 (13), 5719 (20), 5723 (13), 5862 (20), 7547 (3), 7549 (1), 7567 (4), 7657 (15), 8038 (11), 8336 (13), 8345 (20), 9250 (4), 9469 (25), 9744 (12), 9962 (4), 9973 (23), 10578 (20), 11116 (11), 11139 (4), 11163 (11), 11169 (12), 11174 (13); Grove 01 (20); Guerra & Liesner 2871 (4); Guillermo, J. & D. Cardenas L. 863 (16); Gutierrez, G. & Barkley 17115 (25).

Haber & Atwood 9163 (20); Haber & Bello 7191 (20); Haber & Hammel 1799 (20); Haber & Zuchowski 9251 (20), 11175 (25); Haber et al. 4979 (20), 10824 (25); Hahn 142 (15), 945 (23); Hammel 122 (2), 778 (21), 3140 (6), 3586 (20), 3781 (6), 4049 (18), 4101 (20), 4298 (14), 4484 (19), 5378 (14), 5607 (7), 6264 (20), 7212 (6), 8123 (18), 8167 (11), 8212 (12), 8270 (20), 8273 (12), 8415 (20), 8606 (20), 8617 (11), 8748 (12), 8784 (4), 8846 (2), 8873 (11), 8874 (25), 9688 (4), 9772 (4), 9922 (20), 10081 (4), 10082 (18), 10449 (20), 12320 (12), **13636 (5),** 13685 (7), 20231 (20); Hammel & D'Arcy 5018 (15); Hammel & Grayum 14169 (1); Hammel & Kernan 16661 (4); Hammel & Trainer 13962 (20), 14211 (20), 14767 (14), 14786 (19), 15836 (25); Hammel et al. 4882 (18), 6871 (20), 14472 (15), 16262 (14), 16397 (7), 17548 (25), 20114 (20); Harling 313 (15); Harling & Andersson 16727 (15), 18898 (15), 19371 (15), 24778 (15); Harmon & Dwyer 4035 (20); Harmon & Fuentes 4740 (20), 6419 (20); Harris 8361 (23); Harris & Neal s.n. (23); Hartman R. 12488 (15); Henny 5 (2), 7 (23); Herbst & S. Ishikawa 5459 (23); Heredia, M. 60 (23); Hernández 473 (26), 542 (20), 605 (20), 1318 (26), 2586 (26); Hernández & Vazquez 551A (20); Herrera 1636 (20), 4116 (18); Herrera, G. et al. 2928 (20); Herrera, H. 245 (19); Heyde & Lux 4654 (20); Higgins, J. 119 (23); Hill, S. 24812 (23); Hitchcock s.n. (23); Hodge 2929 (23); Hodge & Hodge 3174 (23); Holm-Nielsen et al. 2769 (15), 25355 (18); Holst 62370 (23); Holstein & Armbruster 20425 (20); Hoover 1324 (15); Hoover et al. 3161 (25), 3968 (25); Horich s.n. (11), s.n. (13); Howard 11564 (23), 11744 (23); Howard & Nevling 16978 (23); Huft & Jacobs 1997 (14).

Ibarra 167 (20), 455 (20), 645 (20); Ibáñez et al. 1829 (26); Ibarra & Cedillo 1804 (20); Iltis et al. 30338 (20); INBio 186 (20); Ingram 1124 (15), **1146 (17),** 1169 (23), **76452 (25).**

Jacobs 2159 (20); Jiménez 103 (18), VI (18); Johnston, I. 1165 (14); Johnston, J. R. 305 (23). Judd et al. s.n. (23); Juncosa 619 (25), 797 (15), 1795 (18), 1898 (18), 1912 (18); Jones, A. & Tejada 275 (15).

Kennedy 455 (15), 1193 (14), 1594 (15), 2661 (15), 3253 (25); Kennedy & Foster 395 (15); Kennedy & Solomon 4629 (20); Kenoyer 188 (14); Kernan 381 (20), 748 (4); Kernan & Phillips 831 (4); Kew 70-76-494 (20); Killip 12154 (15), 35113 (18), 39979 (14); Knapp 1042 (19), 2165 (4), 2275 (15), 5758 (6); Knapp & Mallet 3089 (15); Knapp et al. 1717 (6); Koshear 59 (4); Kress 77-830 (15), 77-831 (15), 84-630 (25), 84-1622 (20), 84-1632 (11); Kufer, J. 394 (20); Kursar & Coley 4 (15); Kvist & Asanza 40756 (18); Kvist et al. 48348 (18).

Lasser 16678 (15); Lavastre 1845 (23); Lazor & Tyson 3492 (15); Lazor et al. 2578 (18); LeClezio 135a (16); Le Goff A. 95 (23); Lehmann s.n. (15), 5311 (15), 8876 (25); Leija & Garza 3341 (20), 5597 (20); Leimbeck, R. 306 (15); Lent 37 (18), 161 (1), 639 (25), 694 (25), 2789 (20), 4042 (25); Lent et al. 3374 (18), Leon 720 (25), 26573 (25); Lewis et al. 1753 (6), 2195 (14), 3251 (14); Liesner 114 (1), 1736 (3), 2871 (4), 14102 (20), 14394 (25); Liesner & A. González 10126 (23); Liesner & Judziewicz 14797 (25); Liesner & Mejía 26236 (20); Liesner et al. 7681 (23), 15035 (20), 15122 (20), 15144 (18), 15330 (25), 15365 (25); Liogier 13307 (23); Liogier & Liogier 20185 (23); Lister & Colchester 272 (23); Lloyd 237 (23); Loiselle 106 (25); (20); Løjtnant & Molau 15839 (15); Lopez Garcia & Martin 122 (26); Lotto s.n. (23); Luteyn 1010 (6), 1203 (15), 3175 (15), 3180 (15), 3188 (6), 3263 (20), 3342 (20), 3385 (18), 4043 (14); Luteyn & Croat 906 (14); Luteyn & Kennedy 1612 (6), 1837 (6); Luteyn & Wilbur 4569 (20); Luther s.n. (23).

Maas et al. 7834 (1); MacDougal 1027 (18), 1090 (20),

3193 (20), 3299 (20), 3303 (24); Madison 589 (20), 627 (20), 705 (24), 712 (20); Madison et al. 5008 (15); Maguire et al. 36461 (23); Marten 789 (4), 831 (20), 848 (3); Martínez 3016 (20); Martínez et al. 22713 (20), 23175 (20), 23474 (20), 23693 (20); Martínez, E. 2287 (26), 13445 (20), 13630 (20), 16131 (20); E. Martínez S. & Aguilar 12435 (20); Matuda 16369 (26), 16765 (26); Maxon et al. 6812 (14), 6820 (14); Mayo & Madison 301 (20); McAlpin 85-33 (4); McDade s.n. (16); McDonagh et al. 433 (15), 439 (15); McDowell 148 (20), 769 (11), 1012 (20); McPherson 7371 (25), 9176 (15), 9829 (18), 9865 (25), 10725 (7), 10958 (14), 11129 (25), 11381 (18), 11401 (18), 11591 (14), 11816 (2), 15037 (14); McPherson & J. Aranda 10095 (2); McPherson & Merello 8143 (19), 8235 (18); Meier et al. 5164 (23); Mejia & Ramirez 9929 (23); Mejia & Zanoni 6614 (23); Mena 190 (20); Mendieta 1-10 (15), 1-101 (15), 1-121 (15); Miller & Schmidt 5551 (23); Miller & Taylor 5937 (23); Miller et al. 753 (15); Miranda, F. 7546 (20); Miyashiro s.n. (23); Montenegro, D. & Chung 1462 (20); Montes s.n. (23); Moore, J. W. 451 (23); Moore Jr. & Bunting 8928 (20), 8933 (20); Mora 51 (25), 70 (18); Moraga 173 (20); Morales 1047 (26), 2035 (13); Morales et al. 5413 (20); Moreno 15290 (26), 16421 (26), 16464 (26), 17142 (24); Moreno & Henrich 8427 (26); Moreno & Robleto 20526 (24); Moreno & Sandino 12855 (25), 12891 (25), 12917 (25), 12955 (25), 12976 (18), 15160 (18); Mori & Bolten 7698 (15); Mori & Gracie 18717 (23); Mori & Kallunki 3591 (15), 6026 (6); Mori et al. 3817 (25), 4184 (7), 6814 (25); Murphy & Jacobs 1289 (20); Moreno, P. & J. Sandino 15160 (18).

Nash, G. 611 (23); Nee 9023 (16), 22595 (20), 23733 (20), 29752 (20), 29993 (20), 41364 (23), 99121 (20); Nee et al. 24759 20), 26103 (20); Neill 1571 (24), 1657 (26), 3629 (24); Neill & Vincelli 3484 (12); Neill et al. 11683 (15); Nelson & Andino 16247 (24); Nelson & Cruz 9215 (20), 9291 (24); Nevling & Gómez-Pampa 1505 (20); Nicolson 2060 (23), 3393 (4); Nilsson & Manfredi 505 (20); Nilsson et al. 377 (25), 632 (25); Noriega & H. Vasquez G. 1353a (20).

Ocampo 3411 (20); **Oersted s.n. (20);** Opler 246 (20); Oppenheimer 67-1-3-1244 (16).

Palacios 11452 (25), 13626 (25); Palacios & Tirado 1287 (25), 11327 (15); Paredes et al. 940 (7); Penéis, D. 633 (25); Pérez 1 (25); Pérez, J. & M. Sosa 671 (23); Peterson 6405 (16); Peterson & Annable 6768 (15); Pfeifer 2124 (24), 2163 (20); Philcox 8231 (23); Picado & Gamboa 134 (20), 138 (1); Pipoly 4479 (24); Pitman & Bass 995 (25); Pittier 2600 (15), 2715 (16), 2836 (20), 3754 (14), **3766 (22), 3838 (16),** 3847 (19), 6845 (15); Pittier & Durand s.n. (1); Plowman 14121 (15); Polanco 1485 (15), 1591 (18); Polanco et al. 1905 (15); Porter et al. 4282 (15); Prance et al. 30247 (23); Prevost 3258 (23), 3382 (23), 3580 (23); Proctor 20987 (23), 32251 (20), 38601 (23).

Quesada 51 (4), 175(20); Quishpe & Dávila 82 (15).

Ramamoorthy et al. 3763 (20); Raven 21532 (4); Read & Watson 84-75 (21); Renson 266 (26); Rentería 10680 (15); Ríos et al. 109 (20); Rivera 623 (20), 758 (20), 1560 (20), 1718 (25); Robles, R. 815 (20), 1142 (25), 1158 (25), 1234 (2), 2090 (4); Robles et al. 2050 (25); Rodríguez, A. & Estrada 142 (20); Rodríguez, G. 32 (20); Rodríguez, J. 262 (15); Rojas et al. 607 (23); Roldan et al. 1199 (18); Romero-Castaneda 6436 (16); Rose et al. 4375 (23); Rueda et al. 4070 (4); Rueda & Coronado 6557 (24).

Salick 8092 (12), 8153 (25); Sanchez 539 (2); Sanders et al. 19322 (20); Sandino 1248 (26); Sandoval & Chinchilla 352 (20); Sargent 340 (23), 643 (23); Schatz 1079 (15); Schatz & Grayum 700 (20), 701 (20), 706 (25); Schipp 386 (20); Schmalzel 1212 (15); Schmalzel & Alverson 1199 (15); Schubert & Rogerson 619 (20); Schultes & Cabrera 17890 (23); Schwerdtfeger 21422 (25); Seler 2389 (26), 2398 (26); Shank & Molina 4288 (25); Shattuck 397 (14); Shepherd 438 (19); Simmonds s.n. (23); Sinaca 830 (20); Sintenis, P. 2793 (23); Skutch 5328 (1); Slane 634 (23); Smith 2239 (20); Smith, C. E., Jr. & H. M. Smith 3389 (6); Smith, D. A. 134 (20); Smith, D. et al. 1059 (25); Smith, H. H. & G. W. Smith 1411 (23); Soejarto & Rentería 3556 (19); Solomon 5761 (23); Sparre 14122 (15), 14556 (15), 15182 (15), 15499 (15), 18326 (18), 19397 (15), 19488 (15); Sparrow & Brewster 108 (20); Spellman et al. 164 (20); Sperry 517 (20), 525 (20), 567 (20), 570 (20); Standley 7700 (20), 7935 (20), 18786 (24), 20085 (20), 21077 (26), 21414 (20), 25700 (24), 26156 (16), 26305 (20), 27224 (15), 27413 (15), 28238 (16), 28732 (16), 29867 (14), 31266 (14), 32242 (20), 32794 (20), 36314 (25), 36739 (4), 36840 (2), 38942 (20), 40223 (20), 40960 (14), 41107 (14), 44754 (20), 52702 (20), 52924 (20), 53146 (24), 53990 (20), 55444 (20), 58291 (20), 60715 (20), 63529 (20), 63620 (20), 65041 (20), 66844 (20), 68724 (26), 72447 (20), 75669 (20), 78161(26), 78523 (20), 79561 (26), 87180 (20), 88988 (20); Standley & Chacón 6701 (24); Standley & Valerio 45008 (20), 45206 (25), 45262 (25), 45592 (20), 46000 (20), 48960 (4), 48997 (25); Stein & Hamilton 990 (6); Stergios et al. 7940 (23); Stern et al. 433 (15); Stevens 6027 (26), 6420 (25), 7457 (24), 8044 (24), 11786 (24), 12311 (24), 13564 (25), 13761 (20), 23642 (11), 24257 (12); Stevens et al. 17591 (26), 20998 (24), 24699 (12); Stevenson, P. 379 (16); Steyermark 31763 (20), 34555 (20), 37153 (20), 37456 (20), 38647 (20), 38775 (20), 41699 (20), 44754 (20), 45410 (20), 45869 (20), 47684 (26), 47908 (20), 49321 (20), 49637 (26), 52070 (20), 60796 (23), 88864 (23), 91896 (23), 94331 (23); Steyermark & Bunting 97728 (23), 105293 (23); Steyermark & Davidse 116647 (23); Steyermark & Liesner 118891 (23), 121834 (23); Steyermark & Rogers 119364 (23); Steyermark et al. 100213 (23), 100239 (23), 100318 (23), 102036 (23), 122412 (23), 124629 (23), 124955 (23), 127204 (23); Stimson 5277 (16); Stone 3317 (20); Stricker 342 (20); Sturrock 352 (23); Sullivan 59 (15), 537 (6), 745 (15); Sytsma 1658 (15), 1695 (18); Sytsma et al. 2414 (15), 4398 (6); Sytsma & Andersson 4573 (6); Sytsma & Antonio 3006 (25).

Taylor 216 (20); Taylor, N. 48 (23); Taylor & Taylor 11660 (18); Tellez et al. 4466 (20), 4875 (25); Thompson 128 (15), 160 (15), 441 (26), 3238 (23), 4593 (15), 4816 (15), 4874 (6), 4937 (2), 4951 (8), 5028 (18); Thorne & Lathrop 40559 (20); Tipaz et al. 2280 (18); Tonduz 503 (25), **9961 (1),** 12874 (25); Trujillo et al. 17397 (23); Tyson 1438 (16), 1443 (15), 4632 (14), 6700 (16); Tyson & Blum 3954 (15), 3997 (15), 3998 (14), 4099 (15); Tyson et al. 4486 (15), 4631 (14), 4701 (16), 4834 (14).

Utley & Utley 1100 (3).

Valerio s.n. (20), 246 (20), 462 (1), 1355 (20), 1356 (20); Valverde 741 (13); Vanderveen 590 (20); Vasquez, M. et al. V-907 (20); Villacorta et al. 314 (20), 408 (20); von Wedel 1438 (2), 2892 (18).

Wagner, R. 558 (23); Webster et al. 12581 (24), 12624 (20), 12625 (20); **Wendland s.n. (26),** 410 (26); Whitefoord 1176 (20), 3284 (20); Whitefoord & Eddy 136 (15), 372 (25); Whitehill 8 (23); Wilbur 28249 (20), 37243 (20), 37337 (20); Wilbur & Jacobs 34819 (20), 34962 (20); Wilbur et al. 15664 (6), 15861 (26); Williams, L. et al.

28479 (13); Witherspoon & Witherspoon 8401 (15); Won s.n. (23); Woodbury et al. s.n. (23); Woodson Jr. & Schery 861 (1); Woodson Jr. et al. 1909 (25).

Yanez et al. 1387 (25); Yuncker 4961 (24); Yuncker et al. 8395 (20), 8551 (24), 8826 (20).

Zak et al. 5383 (15), 5414 (15), 5726 (15); Zambrano & Delgado 1336 (14); Zanoni & Pimentel 23420 (23), 23456 (23); Zanoni et al. 23113 (23), 25159 (23), 27170 (23); Zapata et al. 289 (19); Zent, E. & S. 2189 (23); Zuñiga 216 (20).

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Volume 91
2004

ALBACH, DIRK C., Mª. MONTSERRAT MARTÍNEZ-ORTEGA, MANFRED A. FISCHER & MARK W. CHASE. Evolution of Veroniceae: A Phylogenetic Perspective 275

AL-SHEHBAZ, IHSAN A. (see Suzanne I. Warwick, Ihsan A. Al-Shehbaz, Connie A. Sauder, David F. Murray & Klaus Mummenhoff) 99

ARROYO, MARY T. KALIN, LOHENGRIN A. CAVIERES & ANA MARÍA HUMAÑA. Experimental Evidence of Potential for Persistent Seed Bank Formation at a Subantarctic Alpine Site in Tierra del Fuego, Chile 357

BARTHLOTT, WILHELM (see Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott) 525

BEENTJE, HENK JAAP (see Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott) 525

BERNHARDT, PETER (see Peter Goldblatt, Ingrid Nänni, Peter Bernhardt & John C. Manning) 186

BRADFORD, JASON C. (see Patrick W. Sweeney, Jason C. Bradford & Porter P. Lowry II) 266

BROWN, GREGORY K. (see Ana Paula Gelli de Faria, Tânia Wendt & Gregory K. Brown) 303

BRUYNS, P. V. & C. KLAK. Revision of the Madagascan Endemic *Stapelianthus* (Apocynaceae) Based on Molecular and Morphological Characters 410

BURGESS, K. S., J. SINGFIELD, V. MELENDEZ & P. G. KEVAN. Pollination Biology of *Aristolochia grandiflora* (Aristolochiaceae) in Veracruz, Mexico 346

CARDONA, FELIPE. Synopsis of the Genus *Spathiphyllum* (Araceae) in Colombia 448

CATALÁN, PILAR (see Pedro Torrecilla, José-Angel López-Rodríguez & Pilar Catalán) 124

CAVIERES, LOHENGRIN A. (see Mary T. Kalin Arroyo, Lohengrin A. Cavieres & Ana María Humaña) 357

CHASE, MARK W. (see Dirk C. Albach, Mª. Montserrat Martínez-Ortega, Manfred A. Fischer & Mark W. Chase) 275

CHATELAIN, CYRILLE (see Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott) 525

CHEN, J. (see R. J. Henny, D. J. Norman & J. Chen) 464

CHIANG, TZEN-YUH, KUO-HSING HUNG, TSAI-WEN HSU & WEN-LUAN WU. Lineage Sorting and Phylogeography in *Lithocarpus formosanus* and *L. dodonaeifolius* (Fagaceae) from Taiwan 207

Clinebell, Richard R., II, Angela Crowe, David P. Gregory & Peter C. Hoch. Pollination Ecology of *Gaura* and *Calylophus* (Onagraceae, Tribe Onagreae) in Western Texas, U.S.A 369

Coelho, Marcus A. Nadruz (see Eduardo G. Gonçalves, Élder A. S. Paiva & Marcus A. Nadruz Coelho) 473

Crisci, Jorge V. (see Liliana Katinas, Jorge V. Crisci, Warren L. Wagner & Peter C. Hoch) 159

Croat, Thomas B. VIII International Aroid Conference, Missouri Botanical Garden, St. Louis, 9–11 August 1999: Introduction 447

Croat, Thomas B. (see Guanghua Zhu & Thomas B. Croat) 593

Croat, Thomas B. Revision of *Dieffenbachia* (Araceae) of Mexico, Central America, and the West Indies 668

Crosby, Marshall R. & James C. Solomon. Statistical Summary of Some of the Activities in the Missouri Botanical Garden Herbarium, 2003 366

Crowe, Angela (see Richard R. Clinebell II, Angela Crowe, David P. Gregory & Peter C. Hoch) 369

Denham, Silvia S. (see Osvaldo Morrone, Silvia S. Denham & Fernando O. Zuloaga) 225

Faria, Ana Paula Gelli de, Tânia Wendt & Gregory K. Brown. Cladistic Relationships of *Aechmea* (Bromeliaceae, Bromelioideae) and Allied Genera 303

Finot, Victor L., Paul M. Peterson, Robert J. Soreng & Fernando O. Zuloaga. A Revision of *Trisetum*, *Peyritschia*, and *Sphenopholis* (Poaceae: Pooideae: Aveninae) in Mexico and Central America 1

Fischer, Manfred A. (see Dirk C. Albach, Ma. Montserrat Martínez-Ortega, Manfred A. Fischer & Mark W. Chase) 275

Gaskin, John F., Farrokh Ghahremani-nejad, Dao-yuan Zhang & Jason P. Londo. A Systematic Overview of Frankeniaceae and Tamaricaceae from Nuclear rDNA and Plastid Sequence Data 401

Ghahremani-nejad, Farrokh (see John F. Gaskin, Farrokh Ghahremani-nejad, Dao-yuan Zhang & Jason P. Londo) 401

Goldblatt, Peter, Ingrid Nänni, Peter Bernhardt & John C. Manning. Floral Biology of *Hesperantha* (Iridaceae: Crocoideae): How Minor Shifts in Floral Presentation Change the Pollination System 186

Gonçalves, Eduardo G. Araceae from Central Brazil: Comments on Their Diversity and Biogeography 457

Gonçalves, Eduardo G., Élder A. S. Paiva & Marcus A. Nadruz Coelho. A Preliminary Survey of Petiolar Collenchyma in the Araceae 473

Gould, Katherine R. & Lena Struwe. Phylogeny and Evolution of *Symbolanthus* and *Wurdackanthus* (Gentianaceae–Helieae) in the Guayana Highlands and Andes, Based on Ribosomal 5S-NTS sequences 438

Gregory, David P. (see Richard R. Clinebell II, Angela Crowe, David P. Gregory & Peter C. Hoch) 369

GUNN, BEE F. The Phylogeny of the Cocoeae (Arecaceae) with Emphasis on *Cocos nucifera* 505

HAEVERMANS, THOMAS, PETRA HOFFMANN, PORTER P. LOWRY II, JEAN-NOËL LABAT & EMILE RANDRIANJOHANY. Phylogenetic Analysis of the Madagascan *Euphorbia* subgenus *Lacanthis* Based on ITS Sequence Data 247

HENNY, R. J., D. J. NORMAN & J. CHEN. Progress in Ornamental Aroid Breeding Research 464

HOCH, PETER C. (see Liliana Katinas, Jorge V. Crisci, Warren L. Wagner & Peter C. Hoch) 159

HOCH, PETER C. (see Richard R. Clinebell II, Angela Crowe, David P. Gregory & Peter C. Hoch) 369

HOFFMANN, PETRA (see Thomas Haevermans, Petra Hoffmann, Porter P. Lowry II, Jean-Noël Labat & Emile Randrianjohany) 247

HONG DE-YUAN & PAN KAI-YU. A Taxonomic Revision of the *Paeonia anomala* Complex (Paeoniaceae) 87

HONG, S.-P. (see L. P. Ronse De Craene, S.-P. Hong & E. F. Smets) 320

HSU, TSAI-WEN (see Tzen-Yuh Chiang, Kuo-Hsing Hung, Tsai-Wen Hsu & Wen-Luan Wu) 207

HUMAÑA, ANA MARÍA (see Mary T. Kalin Arroyo, Lohengrin A. Cavieres & Ana María Humaña) 357

HUNG, KUO-HSING (see Tzen-Yuh Chiang, Kuo-Hsing Hung, Tsai-Wen Hsu & Wen-Luan Wu) 207

JANSEN, STEVEN (see Frederic Lens, Kathleen A. Kron, James L. Luteyn, Erik Smets & Steven Jansen) 566

KATINAS, LILIANA, JORGE V. CRISCI, WARREN L. WAGNER & PETER C. HOCH. Geographical Diversification of Tribes Epilobieae, Gongylocarpeae, and Onagreae (Onagraceae) in North America, Based on Parsimony Analysis of Endemicity and Track Compatibility Analysis 159

KEATING, RICHARD C. Vegetative Anatomical Data and Its Relationship to a Revised Classification of the Genera of Araceae 485

KEATING, RICHARD C. Systematic Occurrence of Raphide Crystals in Araceae 495

KEVAN, P. G. (see K. S. Burgess, J. Singfield, V. Melendez & P. G. Kevan) 346

KLAK, C. (see P. V. Bruyns & C. Klak) 410

KRON, KATHLEEN A. (see Frederic Lens, Kathleen A. Kron, James L. Luteyn, Erik Smets & Steven Jansen) 566

KÜPER, WOLFGANG, JAN HENNING SOMMER, JON C. LOVETT, JENS MUTKE, HANS PETER LINDER, HENK JAAP BEENTJE, RENAAT SYLVA ANGÈLE ROSINE VAN ROMPAEY, CYRILLE CHATELAIN, MARC SOSEF & WILHELM BARTHLOTT. Africa's Hotspots of Biodiversity Redefined 525

LABAT, JEAN-NOËL (see Thomas Haevermans, Petra Hoffmann, Porter P. Lowry II, Jean-Noël Labat & Emile Randrianjohany) 247

LENS, FREDERIC, KATHLEEN A. KRON, JAMES L. LUTEYN, ERIK SMETS & STEVEN JANSEN. Comparative Wood Anatomy of the Blueberry Tribe (Vaccinieae, Ericaceae s.l.) 566

LIEDE, SIGRID & ULRICH MEVE. Revision of *Metastelma* (Apocynaceae–Asclepiadoideae) in Southwestern North America and Central America 31

LINDER, HANS PETER (see Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott) 525

LONDO, JASON P. (see John F. Gaskin, Farrokh Ghahremani-nejad, Dao-yuan Zhang & Jason P. Londo) 401

LÓPEZ-RODRÍGUEZ, JOSÉ-ANGEL (see Pedro Torrecilla, José-Angel López-Rodríguez & Pilar Catalán) 124

LORENCE, DAVID H. & GERMINAL ROUHAN. A Revision of the Mascarene Species of *Elaphoglossum* (Elaphoglossaceae) 536

LOVETT, JON C. (see Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott) 525

LOWRY, PORTER P., II (see Thomas Haevermans, Petra Hoffmann, Porter P. Lowry II, Jean-Noël Labat & Emile Randrianjohany) 247

LOWRY, PORTER P., II (see Gordon McPherson & Porter P. Lowry II) 260

LOWRY, PORTER P., II (see Patrick W. Sweeney, Jason C. Bradford & Porter P. Lowry II) 266

LUTEYN, JAMES L. (see Frederic Lens, Kathleen A. Kron, James L. Luteyn, Erik Smets & Steven Jansen) 566

MANNING, JOHN C. (see Peter Goldblatt, Ingrid Nänni, Peter Bernhardt & John C. Manning) 186

MARTÍNEZ-ORTEGA, M^A. MONTSERRAT (see Dirk C. Albach, M^a. Montserrat Martínez-Ortega, Manfred A. Fischer & Mark W. Chase) 275

MCPHERSON, GORDON & PORTER P. LOWRY II. *Hooglandia*, a Newly Discovered Genus of Cunoniaceae from New Caledonia 260

MELENDEZ, V. (see K. S. Burgess, J. Singfield, V. Melendez & P. G. Kevan) 346

MEVE, ULRICH (see Sigrid Liede & Ulrich Meve) 31

MORRONE, OSVALDO, SILVIA S. DENHAM & FERNANDO O. ZULOAGA. Revisión Taxonómica del Género *Paspalum* Grupo Eriantha (Poaceae, Panicoideae, Paniceae) 225

MUMMENHOFF, KLAUS (see Suzanne I. Warwick, Ihsan A. Al-Shehbaz, Connie A. Sauder, David F. Murray & Klaus Mummenhoff) 99

MURRAY, DAVID F. (see Suzanne I. Warwick, Ihsan A. Al-Shehbaz, Connie A. Sauder, David F. Murray & Klaus Mummenhoff) 99

MUTKE, JENS (see Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott) 525

NÄNNI, INGRID (see Peter Goldblatt, Ingrid Nänni, Peter Bernhardt & John C. Manning) 186

NORMAN, D. J. (see R. J. Henny, D. J. Norman & J. Chen) 464

PAIVA, ÉLDER A. S. (see Eduardo G. Gonçalves, Élder A. S. Paiva & Marcus A. Nadruz Coelho) 473

PAN KAI-YU (see Hong De-Yuan & Pan Kai-Yu) 87

PETERSON, PAUL M. (see Victor L. Finot, Paul M. Peterson, Robert J. Soreng & Fernando O. Zuloaga) 1

RANDRIANJOHANY, EMILE (see Thomas Haevermans, Petra Hoffmann, Porter P. Lowry II, Jean-Noël Labat & Emile Randrianjohany) 247

ROMPAEY, RENAAT SYLVA ANGÈLE ROSINE VAN (see Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott) 525

RONSE DE CRAENE, L. P., S.-P. HONG & E. F. SMETS. What Is the Taxonomic Status of *Polygonella*? Evidence of Floral Morphology 320

ROUHAN, GERMINAL (see David H. Lorence & Germinal Rouhan) 536

SAUDER, CONNIE A. (see Suzanne I. Warwick, Ihsan A. Al-Shehbaz, Connie A. Sauder, David F. Murray & Klaus Mummenhoff) 99

SINGFIELD, J. (see K. S. Burgess, J. Singfield, V. Melendez & P. G. Kevan) 346

SMETS, E. F. (see L. P. Ronse De Craene, S.-P. Hong & E. F. Smets) 320

SMETS, ERIK (see Frederic Lens, Kathleen A. Kron, James L. Luteyn, Erik Smets & Steven Jansen) 566

SOLOMON, JAMES C. (see Marshall R. Crosby & James C. Solomon) 366

SOMMER, JAN HENNING (see Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott) 525

SORENG, ROBERT J. (see Victor L. Finot, Paul M. Peterson, Robert J. Soreng & Fernando O. Zuloaga) 1

SOSEF, MARC (see Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott) 525

STRUWE, LENA (see Katherine R. Gould & Lena Struwe) 438

SWEENEY, PATRICK W., JASON C. BRADFORD & PORTER P. LOWRY II. Phylogenetic Position of the New Caledonian Endemic Genus *Hooglandia* (Cunoniaceae) as Determined by Maximum Parsimony Analysis of Chloroplast DNA 266

TORRECILLA, PEDRO, JOSÉ-ANGEL LÓPEZ-RODRÍGUEZ & PILAR CATALÁN. Phylogenetic Relationships of *Vulpia* and Related Genera (Poeae, Poaceae) Based on Analysis of ITS and *trn*L-F Sequences 124

WAGNER, WARREN L. (see Liliana Katinas, Jorge V. Crisci, Warren L. Wagner & Peter C. Hoch) 159

WARWICK, SUZANNE I., IHSAN A. AL-SHEHBAZ, CONNIE A. SAUDER, DAVID F. MURRAY & KLAUS MUMMENHOFF. Phylogeny of *Smelowskia* and Related Genera (Brassicaceae) Based on Nuclear ITS DNA and Chloroplast *trn*L Intron DNA Sequences 99

WENDT, TÂNIA (see Ana Paula Gelli de Faria, Tânia Wendt & Gregory K. Brown) 303

WU, WEN-LUAN (see Tzen-Yuh Chiang, Kuo-Hsing Hung, Tsai-Wen Hsu & Wen-Luan Wu) 207

ZHANG, DAO-YUAN (see John F. Gaskin, Farrokh Ghahremani-nejad, Dao-yuan Zhang & Jason P. Londo) 401

ZHU, GUANGHUA & THOMAS B. CROAT. Revision of *Dracontium* (Araceae) 593

ZULOAGA, FERNANDO O. (see Victor L. Finot, Paul M. Peterson, Robert J. Soreng & Fernando O. Zuloaga) 1

ZULOAGA, FERNANDO O. (see Osvaldo Morrone, Silvia S. Denham & Fernando O. Zuloaga) 225

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CONTENTS

Africa's Hotspots of Biodiversity Redefined ——— *Wolfgang Küper, Jan Henning Sommer, Jon C. Lovett, Jens Mutke, Hans Peter Linder, Henk Jaap Beentje, Renaat Sylva Angèle Rosine Van Rompaey, Cyrille Chatelain, Marc Sosef & Wilhelm Barthlott* 525

A Revision of the Mascarene Species of *Elaphoglossum* (Elaphoglossaceae) ——— *David H. Lorence & Germinal Rouhan* 536

Comparative Wood Anatomy of the Blueberry Tribe (Vaccinieae, Ericaceae s.l.) ——— *Frederic Lens, Kathleen A. Kron, James L. Luteyn, Erik Smets & Steven Jansen* 566

Revision of *Dracontium* (Araceae) ——— *Guanghua Zhu & Thomas B. Croat* 593

Revision of *Dieffenbachia* (Araceae) of Mexico, Central America, and the West Indies ——— *Thomas B. Croat* 668

Checklist for Authors ——— 773

Index for Volume 91 ——— 779

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